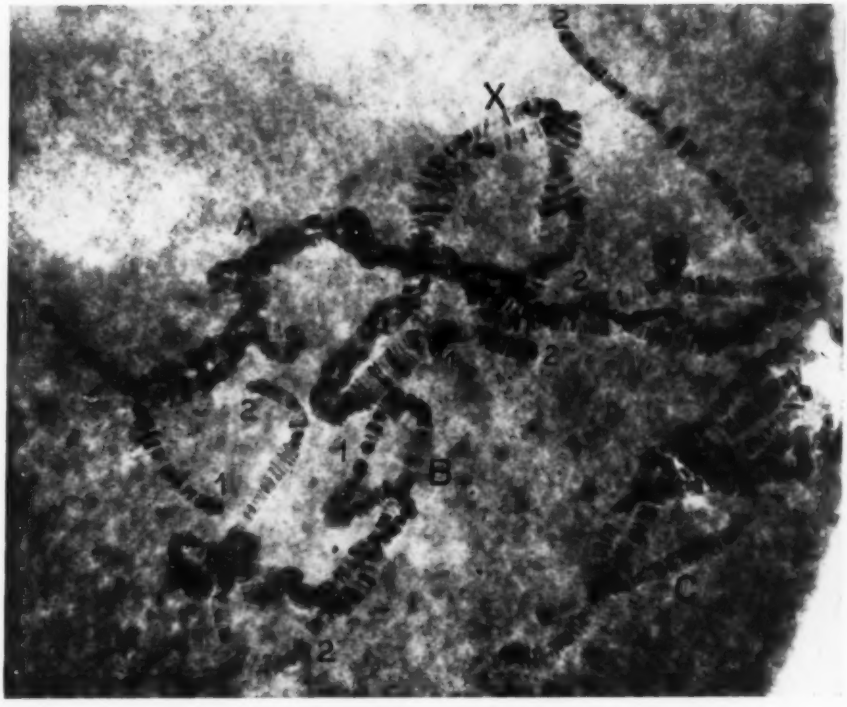
PEARL

The Journal of HEREDITY



CHROMOSOME-PAIRING IN A SPECIES HYBRID
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From Ape to Moron

Hairless Siamese Cats

Mutations in the Pineapple

Sex- and Caste-Determination in Ants

A Colchicine-Tetraploid in the Zinnia

Inheritance of Hydrocephalus in Swine

VOLUME 29 MAY, 1938 NUMBER 5

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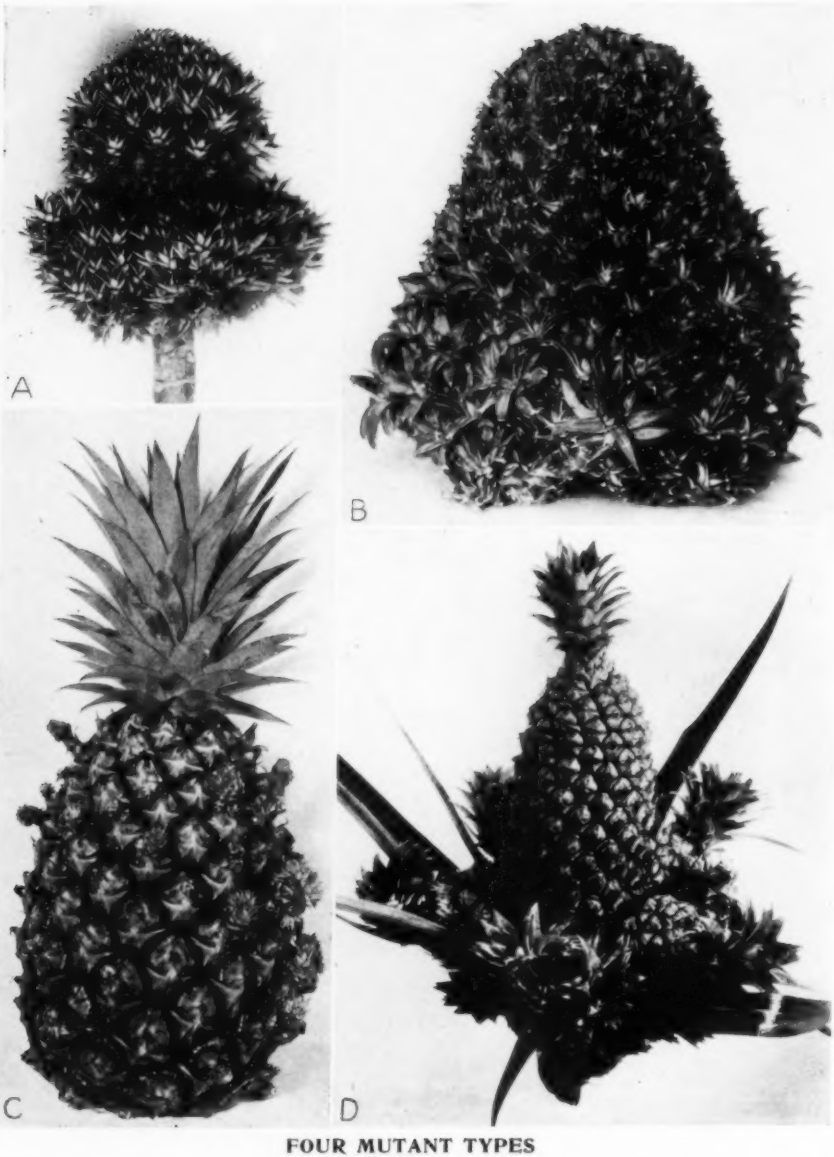


FOUR MUTANT TYPES

Frontispiece

Since 1930 a study of mutant types of the Cayenne variety of pineapple has brought to light thirty variations which appear to be genetic in origin. The four odd forms shown here are all due to modification of the flower,—the pineapple "fruit" being a collection of sterile inflorescences, with usually seedless fleshy carpals. *A*—Shows the *Hourglass* mutation, in which the middle third of the fruit is normal, while the ends are covered with floral prolifications similar to those found over all the fruit in the mutation *Crowning Beauty* (shown at *B*). Here the normal flower parts of each floret are replaced by leaves of the type found in the crown of the normal pineapple. *C*—The *Slipping Beauty* mutant, in which the floral parts are replaced by slip-like prolifications instead of the crown leaves as found in the two mutations described above (*A, B*). In the *Collar-of-Slips* variation (*D*), this form of prolification is confined to the base of the fruit and the slips are larger. *Crowning Beauty* and *Collar of Slips* are dominant in crosses.

MUTATIONS IN THE PINEAPPLE

A Study of Thirty Inherited Abnormalities in the Cayenne Variety

J. L. COLLINS AND K. R. KERNS*

IN Hawaii the most important variety of the pineapple [*Ananas Comosus* (L.) Merr.] is the Cayenne. There is no authentic record of the origin of the Cayenne variety, but it can be assumed with assurance that the variety started as the vegetatively reproduced progeny of a single hybrid plant about 100 years ago. Originally a single clone it in time became a collection of clones through the process of mutations giving rise to new types, some of which were perpetuated by the asexual method of reproduction common in this variety.

Natural and artificial selection has, no doubt, eliminated some of the more extreme mutant types. The present collection of mutant types represents that portion of the total mutations which were able to survive in the general population because of their vigor or general similarity to the type, or those having a high rate of mutation by virtue of which they frequently reappear in the general population although they generally fail to be reproduced for any length of time because of their inferiority or conspicuousness.

The presence of certain abnormal types in the general population had been known for a long time; some had even been isolated as clones in the course of early plant selection work. In 1930 a definite effort was commenced to collect and progeny test these variant types in order to make a more systematic study of their genetical and morphological nature and to segregate genetic types from modifications which were not inherited.

The purpose of the present paper is primarily to describe and record the origin or discovery of these mutant types. Brief mention will be made of the genetic nature of some, but the data upon which the genetic conclusions rest will be presented in a more detailed account of individual mutants. The mutants listed in Table 1 have all been tested through two or more vegetative generations.

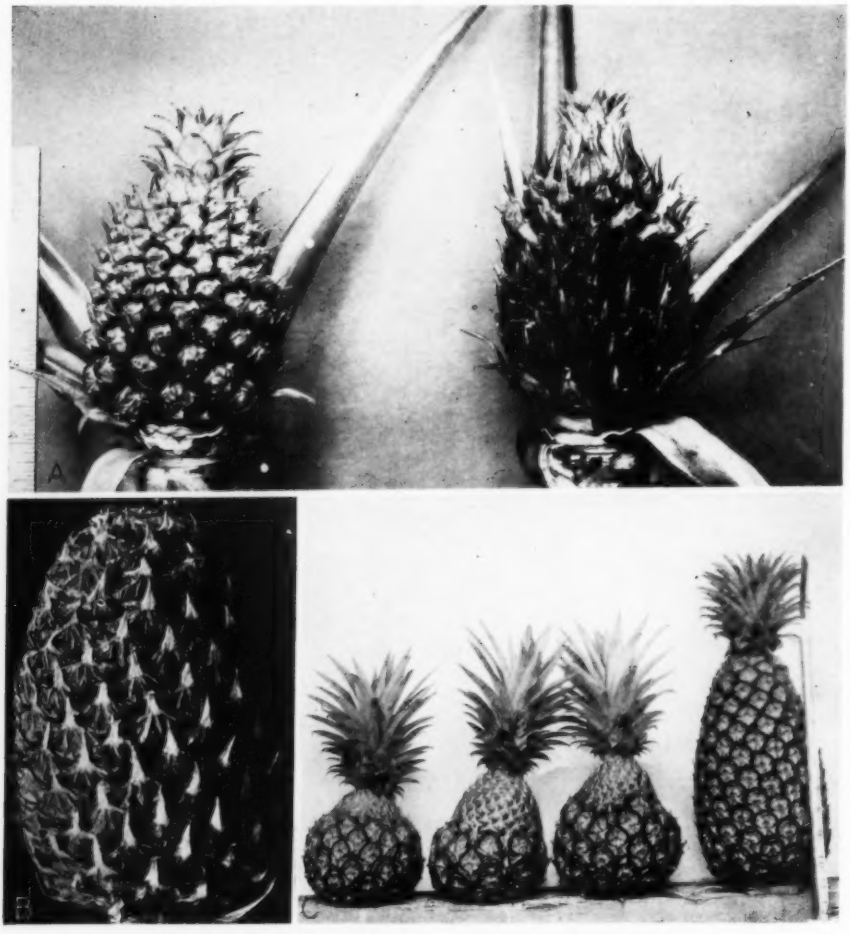
Description of Mutations

1. *White Flowers:* The normal color of the petals is bluish-purple. The white mutant was first located March 7, 1934, at the Wahaiwa Experiment Station. Two plants having white flowers were found in a population of eight plants of Accession M4, a mutant type lacking anthocyanin pigment. On one of the two plants all the flowers were white, but on the other plant one blossom was a chimera, one-half of the two petals being white; while the third petal was normal in color. A clone of white flowered plants has been established from one plant having all flowers white, and crosses have been made between it and the normal bluish-purple flowered plants. The F_1 plants flowering in 1937 had very pale blue flowers, indicating a lack of complete dominance of the normal blue-purple character.

2. *Flowering Beauty:* (Figure 1*A*.) Clone originated from a single plant found† about 1928. A second occurrence, probably of independent origin, was noted on the Island of Lanai in October, 1931. In this type the petals are increased many times in number together with complete failure of essential floral elements to develop including the carpels. The fruitlets are enlarged and protruding, giving a rough surface to the enlarged fruit. The entire interior of the fruit is core-like in texture and

*Published with the approval of the Director as Technical Paper No. 89 of the Pineapple Experiment Station, University of Hawaii.

†Found by M. O. Johnson, Wahiawa, Oahu, and given to the authors in 1930.



FLOWER ABNORMALITIES IN THE PINEAPPLE

Figure 1

A—Flowering Beauty mutant on the left, normal inflorescence on the right. In the former the petals are increased to many times the normal number, but the rest of the flower is abortive. In the *Dry Fruit* mutation (*B*), all floral structures are absent or abortive except the bracts giving a fish-scale effect. In the *Bottle Neck* variation (*C*), only the upper part of the inflorescence exhibits the *Dry Fruit* type of flower abortion. A normal fruit is shown on the right.

completely lacking in the characteristic flavor. Genetic analysis is precluded by the complete absence of essential floral elements.

3. *Dry Fruit and Bottle Neck:* (Figure 1*B* and 1*C*.) First selected in 1924 and has been located a number of times subsequently. In the dry fruit all floral parts are either completely absent or present in a vestigial and non-functional condition. Only the bract, normally subtending the floret, is present in an imbricated condition, giving the suggestion of fish scales. Such fruits con-

sisting only of the receptacle, are about one-half natural size with a non-edible, core-like interior.

The *Bottle Neck* (Figure 1*C*) is similar to the Dry Fruit except that from a few to one-half or more of the florets are normal and develop into normal fruitlets. There is a marked reduction in diameter at the transition zone between normal fruitlets and the receptacle area which produces the Bottle Neck appearance.

The two types are listed together because one may sometimes give rise to the other. The Dry Fruit type sometimes produces fruits with a few normally developed fruitlets while the Bottle Neck type occasionally produces a Dry Fruit.

4. *Crowning Beauty, foliar floret prolification:* (Frontis.-*B*.) Originated as a single plant in 1929, from which a clone was established. Floral structures of each floret are replaced with foliage leaves of the crown type. Each fruitlet of the multiple fruit develops a small crown analogous to the crown of the normal inflorescence. The fruit of this type is fibrous, core-like and lacking in edible qualities. Variations occur in the direction of normal florets, some of which produce viable gametes. These variants have made it possible to test this type genetically. Since approximately 50 per cent of the F_1 progeny produced by pollinating normal fruited plants with pollen from variants of the Crowning Beauty clone showed foliar prolifications, it is concluded that this type arose from a single dominant gene mutation and the plants of this clone are heterozygous for the recessive normal type.

5. *Hourglass, foliar floret prolification:* (Frontis.-*A*.) Located in 1933 as a single plant. The middle one-third of the fruit had normally or almost normally developed fruitlets while those at the base and top thirds had developed foliar prolification similar to Crowning Beauty. However, this form reproduces the Hourglass type by vegetative propagation while the former reproduces the Crowning Beauty type.

6. *Slipping Beauty, foliar floret prolification:* (Frontis.-*C*.) These fruitlet prolifications are distinctly different from those listed above (4 and 5); first in the irregular occurrence of prolification among the fruitlets and second in the type of prolificated growth which is more nearly allied to the development of the slips than crowns of the normal plants. The prolificated portion is usually insecurely attached to the fruitlet by a short pedicel or stalk. Above this stalk is produced a small scaly bulb or ball similar to the scaly ball commonly produced at the base of slips. Growing from this ball are small short leaves, also analogous to the leaves of regularly produced slips. The essential floral organs are absent and the interior of the fruit is core-like in texture.

7. *Multiple Sepals and Bracts:* (Figure 3D.) First recorded in 1932 but reported as being seen two or three years earlier. It has subsequently been reported from several widely separated areas. Normal fruitlets have three triangular-shaped sepals with acuminate, scabrous tip subtended by a single similarly shaped fleshy bract. In this mutant type the number of bracts and sepals is increased from 1 to 5 times and accompanied with sepaloidy. Aside from the bristly appearance caused by the increased number of sepals and bracts, the fruits are normal.

8. *Elongated Bracts and Sepals:* First recorded in 1930 but had also been seen at an earlier time. Since it was first recorded and described, it has been found several times in fields. In this type the bracts and sepals are normal in number but have increased in length until they lend a decided pointed appearance to the fruitlet in developing fruits. The elongated parts are less conspicuous in ripe fruits due to drying and shriveling of the sepal and bract tips.

9. *Big Eye:* (Figure 3*B*.) First recorded in 1931, but it was found and isolated as a clone by M. O. Johnson at an earlier date. Since 1931 it has been reported a number of times from widely separated localities. Fruitlets are enlarged and as a consequence the whole fruit. The sur-

face of the fruitlet is very much roughened and wrinkled and the fruit flesh is coarse and fibrous. The lenticel-like scars on the sepals and bracts are increased in number and size. The ripening of the fruit is delayed in comparison with normal fruits. This is a very unstable character, conspicuous chimeras often appearing having vertical sectors of normal fruitlets with their smaller size and smoother surface. Such normal sectors ripened earlier than the surrounding enlarged eye parts. While these fruits have the appearance of polyploids the plants on which they are produced are diploid.

10. *Slender Fruit (small diameter):* (Figure 3*E*.) Recognized as an hereditary variant as early as 1924. It is characterized chiefly by the smaller than normal diameter of the fruit. It also frequently has protruding fruitlets developed at the base of the multiple fruit.

11. *Seedy Fruit:* Fruits of the Cayenne variety are normally seedless. Mutants of several types have been isolated as clones which regularly produce from a few to many seeds. In a few instances where cross pollinations have been made the results indicate that the change is a dominant one and the mutant types are heterozygous for the dominant seedy character.

12. *Elongated Fruit:* Selected from the field population by M. O. Johnson, this clone differs slightly but consistently in fruit shape which gives the appearance of a longer than normal fruit. It has maintained its character through many vegetative generations of reproduction and is considered as a progressive mutation.

13. *Rough Eye:* (Figure 3*A*.) Originally selected in 1924 and continued as a clone. The fruit is characterized by a fruitlet surface which is slightly more elevated or protruding at the middle than is normal for the variety. In this respect the surface of the fruit is more like the surface of the Queen variety which has pronounced central protrusion of the fruitlet surface. This change is in the direction of a character common to another variety.

14. *Collar-of-Slips:* (Frontis.-D.) Recognized as distinct and hereditary as early as 1924. It is characterized chiefly by the presence of foliar branches (slips) developing from the axils of involucral leaves. These branches are frequently attached directly to the fruit as an outgrowth from a fruitlet at the base of the fruit. This type is subject to a wide range of variation in development, and may even be completely suppressed in some plants. The degree of expression is known to be correlated with certain environmental conditions. Results from hybridizations indicate that the character is dominant and in this clone heterozygous.

15. *Spiny Leaves:* The variety name Smooth Cayenne has reference to the absence of spines on the leaves. The leaves do have a few spines near the tip, however. This spiny leaved type arises by mutation from the heterozygous dominant smooth type to the homozygous recessive spiny. This change occurs frequently and spiny plants and spiny-smooth chimeras are common.

16. *No Anthocyanin:* The variety commonly has anthocyanin in the upper epidermis of the leaves, stem and fruit. Hereditary variations in anthocyanin have been known for a long time. The most common is that in which the pigment fails to develop in the leaves only. This mutation represents a single change from the heterozygous dominant normal to the recessive homozygous *no anthocyanin* condition.

17. *Linear Anthocyanin:* A fairly commonly appearing hereditary reduction in anthocyanin, the latter appearing in narrow linear streaks or ribbons. This type is frequently found in chimeras, the other part of the plants being either normal or *no anthocyanin*.

18. *Blush:* Anthocyanin appearing only in the involucral bracts subtending the inflorescence.

19. *Intensified Anthocyanin:* Located as three plants near each other in a Molokai field in 1936. These were considered to be the progeny of a single plant in the preceding vegetative generation. They have retained this plus an-

thocyanin character in the third generation. In addition to a change in pigment intensity these plants are also of the *slender fruit* type. The normal plants of the variety are known from genetic tests to be heterozygous for *no anthocyanin*. In selfing plants of the Cayenne variety and in certain varietal crosses with it as one parent, homozygous anthocyanin segregants have been obtained to which the present mutant plants are similar in appearance. The *intensified anthocyanin* type is believed to have originated from a dominant mutation of *Aa* to *AA*, thus producing a homozygous gene condition from the heterozygous one.

20. *Albino (absence of chlorophyll)*: Occurs in vegetative reproduction almost always as a chimera, which takes the form usually of no chlorophyll in leaf margins or leaf center; less frequently it appears as sectorial chimeras. The variety is heterozygous for seedling albinism and the mutation represents a change to the homozygous recessive condition.

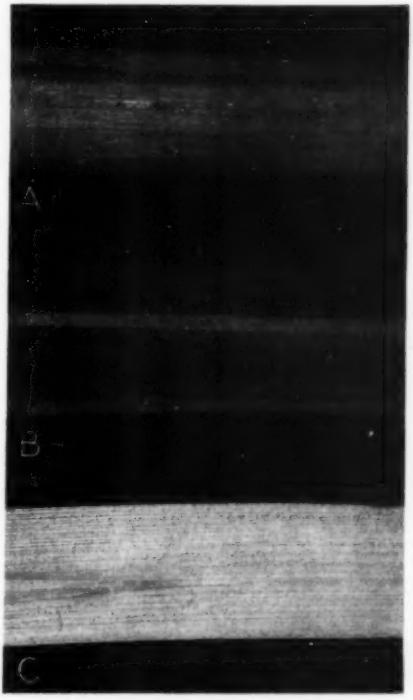
21. *Streaked Chlorophyll:* Chlorophyll reduced in narrow linear streaks alternating with streaks of dark normal green color.

22. *Waxy (absence of trichomes)*: (Figure 2.) The absence of trichomes on the lower epidermis of the leaves gives a waxy, dark-green appearance to the leaves. Waxy plants are also usually less vigorous than normal plants.

23. *Semi-Waxy:* Trichomes reduced in number and present only in the grooves between fiber strands.

24. *Increased:* Trichomes appear to be more numerous and dense on the lower leaf surface and also are sparsely present on the upper epidermis where they do not occur normally.

25. *Black Streak:* A linear black streak about 2 to 3 millimeters wide appearing on the upper or lower surface of the leaf (sometimes on both sides). At the location of the streak the epidermis is absent and the color is due to the development of pigmented cork cells at the place where unprotected thin-walled mesophyll cells are exposed. The absence of epidermis is believed to be due to a dominant cell lethal mutation which causes the death of the cell in which it occurs. When such a mutation occurs in a primordial epidermis cell, the cell is killed and the neighboring cells continue to grow, leaving a vacant ribbon where the progeny of the dead cell would have been.

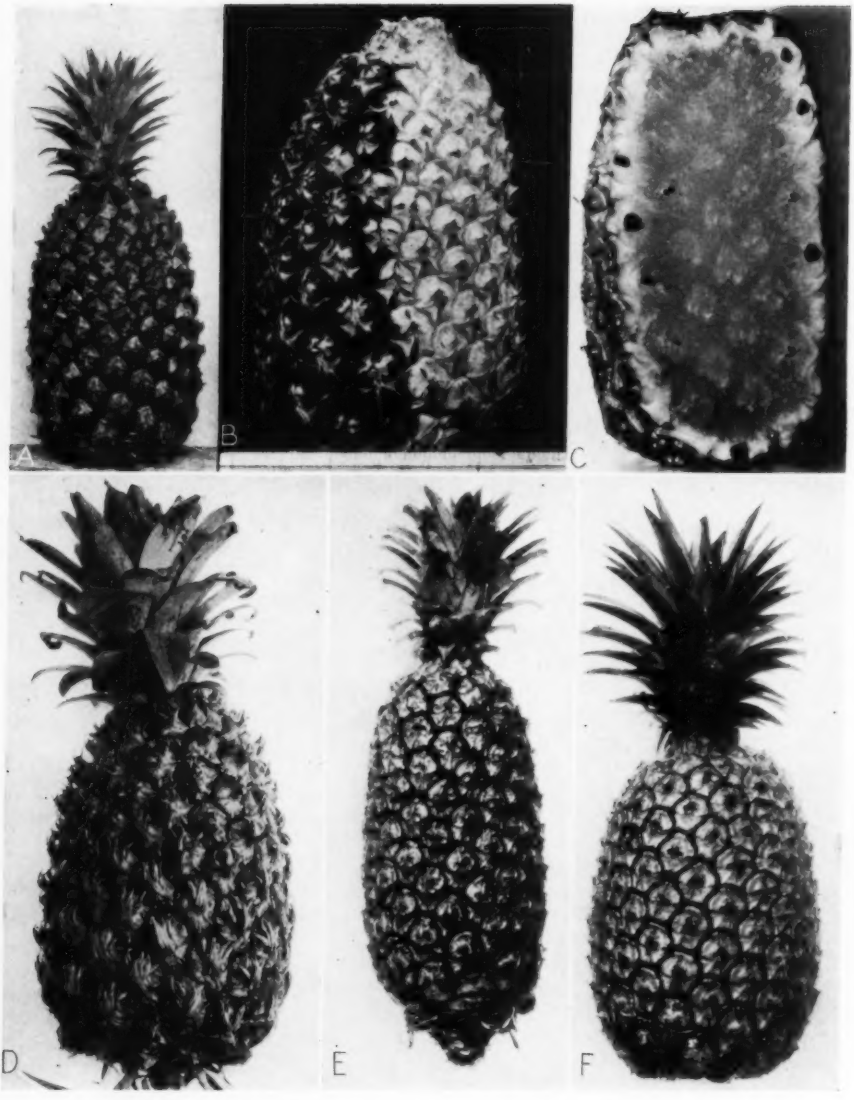


THE WAXY VARIANT

Figure 2

Sections of leaves showing (*A*) *Waxy* mutation (absence of trichomes), as compared with (*C*) normal development of hairs on the lower surface of the leaf. The waxy leaf in the center (*B*) has a linear stripe of normal trichomes.

26. *Blooming Blomfield (BB)*: (Figure 4*C*.) A gigas type of plant which differs from the normal in number and length of leaves; angle of leaves with main plant axis; development of spines; size of fruit and length of vegetative period. It is a dominant mutation heterozygous in genotype. First reported



CHANGES IN FRUIT AND EYE STRUCTURE

Figure 3

A—Rough-eye mutation, to be compared with normal smooth-eyed fruit (*F*). *B*—Chimera showing *Big Eye* mutation on left half of the fruit—normal on right. The normal fruit has cavities in the carpels to accommodate the seeds. These are lacking in the *Non Porous* mutation (*C*). The rough fruit of *Multiple Sepals and Bracts* (*D*) is normal in internal structure but the sepals and bracts are increased greatly in number. *E—Slender*, a mutant in fruit form maintained since 1924. *F*—Normal Cayenne.

on Oahu in 1922 when three plants were found in the same field.

27. *Lanai:* (Figure 4*A*.) A semi-dwarf type which differs from the normal mainly in having more but shorter leaves. It is a dominant mutation having a heterozygous genotype. The angle of the leaves with the plant axis is more acute than in the normal plant. First reported as a single plant from the Island of Lanai in 1934.

28. *Paper Leaf:* (Figure 4*D*.) A mutant type characterized by a number of simultaneous character changes. The plants and fruits are dwarf; the leaves are sharply recurved and have anthocyanin in linear stripes. The chlorophyll appears to be reduced resulting in a pale yellowish green leaf color. Fruits are small and poor in quality.

29. *Driver's Dwarf:* First located in a Molokai plantation field in 1934. Plants and fruits are small. Anthocyanin is very dilute and present in the streaked type. The chlorophyll is also distributed in alternate narrow linear streaks of normal and light green. The fruits are of the *Collar-of-Slips* type.

30. *Non-Porous:* (Figure 3*C*.) A mutant type characterized by a very solid non-porous fruit. The normal fruit has small cavities in the carpels where seeds develop in the fertilized florets. In this mutant these carpel cavities are filled, leaving no seed space. This is considered as a progressive mutation.

Discussion

Thirty mutant types have been shown by progeny tests to be transmitted through successive generations of vegetative reproduction. Eight types have been reproduced through sexual reproduction. *Seedy Fruit, Collar-of-Slips, Crowning Beauty, Lanai* and *Blooming Blomfield* type mutations are dominant over the normal characters while the mutations involving spiny leaves, loss of anthocyanin and loss of chlorophyll are recessive to the normal characters for the variety.

Three other characters are probably dominant mutations but they have not been tested genetically. One mutant, *Black Streak*, cannot be tested for it appears to be lethal, killing the cell in which the mutation occurs. The growth and development of leaf epidermis is such that it permits the effect of such a dominant lethal to become evident when it occurs in a primordial epidermis cell.

The variety has been shown to be heterozygous for anthocyanin pigment in the epidermis. Mutations preventing the development of this pigment are recessive. The Intensified Anthocyanin mutation (No. 19 on page 166) may therefore represent a dominant change since it is in the opposite direction. In a similar way *Increased* (superabundance of trichomes) (No. 24 on page 167) may also represent a dominant mutation although the genetic nature of the variations in bloom development are not known with certainty. White Flowers appears to be a partially dominant character since the cross with a normal purple flowered variety the flower color of the F_1 is very pale blue.

Blooming Blomfield, Lanai, Paper Leaf and *Driver's Dwarf* constitute an interesting series of mutant types because in each case not one but a number of distinct characters have changed simultaneously. They are all diploids but there is a possibility that they may represent types in which some kind of chromosomal aberration has taken place without change in chromosome number, such as the new types of *Datura* synthesized by Blakeslee, Bergner and Avery (1936). Fertility is greatly reduced in the *Paper Leaf* but is good in *Blooming Blomfield* and *Lanai* types.

The large percentage of dominant mutations found in this variety is of interest because dominant genetic changes are generally very rare relative to the number of recessive changes in a species. Because of this unusual situation it is necessary to examine carefully the evidence which indicates dominance of these mutant types.

The failure to find these dominant mutant types in the selfed progeny of Cayenne is the best evidence that they have not been carried in the genotype as recessives. On the other hand a number of

DWARF AND GIANT FORMS

Figure 4

Typical plants of: *A—Lanai; B*—Normal Cayenne; and *C—Blooming Blomfield. Paper Leaf* (*D*) is a chlorophyll-deficient dwarf with fruits of poor quality. The *Lanai* and *Blooming Blomfield* mutations are dominant in crosses, the mutant plants being heterozygous for the recessive mutant genes.

the characters which have appeared as mutants in vegetatively propagated populations have appeared among the seedlings resulting from self fertilization of the variety. Thus the *Intensified Anthocyanin* (No. 19 on page 166), which appeared as a mutation in vegetatively reproduced plants is considered to be the result of a dominant change because the variety is known to be heterozygous for anthocyanin production and the mutant is similar in appearance to the homozygous anthocyanin segregants which have appeared in seed progeny of Cayenne. The *Intensified Anthocyanin* is, therefore, believed to have originated by a change in the genotype, *Aa* to *AA*. The graded variation of anthocyanin mutants suggests a multiple allelomorphic series of genes influencing this character.

Plants of the dominant *Crowning Beauty* type have never been found in several hundred thousand sexually produced normal plants of *Ananas*, yet in a single population produced by crossing the *Crowning Beauty* (pollen parent) with normal plants of the Natal variety, approximately 50 per cent of the F_1 progeny were the *Crowning Beauty* type.

The semi-dominance of the white flowered mutant is based upon two lines of evidence. First, white flowered plants have never appeared in selfed or crossed Cayenne progeny and it is therefore unlikely that the gene is present in the genotype of the variety as a recessive. The second line of evidence comes from the flower color of the F_1 hybrids which is very pale blue, essentially an intermediate color between that of the parents.

The *Lanai, Blooming Blomfield* and *Collar-of-Slips* types when crossed with plants of normal type produce about 50 per cent of their own type in F_1 but these types have not appeared in selfed progene of Cayenne. The *Collar-of-Slips* type in the Taboga variety is dominant and homozygous as indicated by the F_1 progeny, all of which show the collar character.

The relative frequency of mutation for the different types is difficult to determine in a vegetatively reproduced form where a small, inconspicuous sector of the mutant may be carried in an otherwise normal plant and only give rise to a complete plant or conspicuous part of a plant after several vegetative generations during which the single original mutation may be distributed to a number of progeny plants.

A high gene mutation rate would result in most cases in a high frequency of appearance, but the latter cannot be considered as a direct index of the former due to the influence which the type of character would have upon the chances that a gene mutation would involve the tissues from which the character originated. A character, such as petal color, would have less chance to show a mutation than one influencing leaf color or size because fewer cells are required in the former. The mutations *Black Streak* and *No Anthocyanin* presumably may occur in any cell in the growing part of the plant but become evident only when cells of the epidermis are involved. It is therefore, primarily frequency of appearance that is considered here. It has been shown (Collins 1936) that the gene for spineless leaves, carried as a heterozygous dominant in this variety, is relatively unstable and mutates frequently to the spiny condition. Spiny plants and spiny-smooth chimeras continue to appear in populations of this variety although roguing selections are constantly carried on to eliminate spiny plants.

Even genes that are quite stable have increased opportunity for mutations to appear when the number of individuals in a population is very large. This condition is fulfilled in the Cayenne variety where approximately 1,800,000,000 shoot meristem areas are produced annually from which the propagating materials (crowns, slips and suckers) for new plants are produced.

The Paper Leaf and Albino types are largely self eliminating because of their low viability, yet plants showing these characters are seen from time to time in populations where their presence can best be explained as due to recent mutation. Both types occur more frequently as chimeras than as complete plants. However, the rate of mutation appears to be much below that for spiny leaves.

A number of the mutants, notably *Lanai, Blooming Blomfield* and *Driver's Dwarf* have been reported once only and it is believed that the rate of mutation giving rise to these characters is very low.

The 30 mutant types listed in Table 1 are relatively conspicuous and easily recognized. It is believed that many other mutant types exist in the variety which differ so little from the normal type that they are within the range of modifications due to environmental variations. As an illustration of this type of minute differences, mention may be made of clones established in this variety having slight differences in green color which become evident only when the plants are

viewed in mass but cannot be recognized in single plants in the general variety population because of the environmental variation existing in the latter. Evidence has also been obtained for the existence of physiological differences particularly in reaction to diseases.

The writers have, largely as a result of their experiences with mutations in this variety, arrived at the conviction that mutations in asexually propagated forms may cause continuous and gradual change in the genotype so that ultimately a variety may contain many genes not originally present and to have lost some of the original ones. Collins[3] in *Ananas* and Banta and Wood[1] in *Cladocera,* have shown that during asexual reproduction there was an accumulation of recessive mutations in the germ plasm which became evident during subsequent sexual reproduction. Muller[4] and later Plough and Child[5] devised and used breeding plans by which recessive mutations could be accumulated and stored up on certain *Drosophila* chromosomes for many generations and later brought into expression by appropriate crossing. Continued asexual reproduction permits the accumulation of mutations in all of the chromosomes.

Plough and Child conclude from their study of the occurrence of lethal mutations in *Drosophila,* "that there is no such thing as a static species in nature." It appears from the study of mutations in *Ananas* that this statement will also apply to asexually propagated forms. The mutations studied in this genus are classified as regressive, progressive, dominant and recessive.

The accumulation of mutations in asexually propagated forms may conceivably play a role in the running out and acclimatization of varieties. The parade of agricultural varieties during the past years is a demonstration of the changes going on, some of which is known to be due to progressive or regressive mutations.

TABLE 1. Classification of mutations in *Ananas* according to part of plant involved with brief description of the change. Deletions underscored are dominant changes; others are recessive.

General character	Normal condition	Mutation	Local name
Anthocyanin	Purple flowers	White flowers	White Flowers
	Perfect flowers	Extreme petal multiplication, with absence of carpels	Flowerless Beauty
	Perfect flowers	Absence or abortion of all floral parts	Dry Fruit and Bottle Head
	Single flower rhombs	Polar floret proliferation: Type A. Lack fruitlet with normal-like leaves.	Branchless Beauty
		Type B. Fan fruitlet with adaptive foliar proliferation.	Elliptic Beauty
		Type C. Like Type A except proliferation confined to top and base parts of fruit	Hourglass proliferation
	3 sepals and one subsepalar bract; 3 colored petals	Virescence, complexity of petals and increase in number of parts	Multiple Sepals and Bracts
	Sepals and bracts short	Increased length of parts	Elongated Sepals and Bracts
Fruit:	Normal size fruitlet	Enlarged fruitlet	Pig Eye
	Smooth flat fruitlet	Pointed protruding fruitlet	Rough Eye
	Normal diameter	Decreased fruit diameter	Slender Fruit
	Seedless	Seeds produced	Seedy Fruits
	Normal length	Increased length of fruit	Elongated Fruit
	Slips on peduncle	Slips attached to fruit base	Collared Slips
	Carpels partly open normally	Carpels completely filled	Non-Porous
Leaves	Smooth margins	Spiny margins	Spiny
	Anthocyanin pigment diff.used over leaf surface	1. In linear ribbons	Linear Anthocyanin
		2. In involucral leaves only	Bluish Anthocyanin
		3. Absent	No Anthocyanin
		4. Increased above normal	Plum or Purple-flecked Anthocyanin
	Normal chlorophyll development	1. Complete absence of chlorophyll	Albino
		2. Reduced amount of chlorophyll in linear streaks	Striated Chlorophyll
	Trichomes abundant giving a silver grey color to under leaf surface.	1. Increased amount of trichomes	Intensified trichomes
		2. Trichomes aborted or vestigial	Waxy (no bloom)
		3. Trichomes present in linear leaf grooves between vascular bundle ridges	Reduced (reduced number of trichomes)
	Normal epidermis	Leaf epidermis absent in linear streaks	Black Streak (cell lethal)
Whole plant	Typical plant	Increased number of leaves with decrease in length	Dwarf
	Typical plant	Increased number of leaves with increased length and width, increased fruit size and period of vegetative growth, increased spininess of leaves. Change in angle of leaf axil with main plant axis.	Blooming Riverside (Ib)
	Typical plant	Reduced plant and fruit size, product leaf habit, reduced chlorophyll, anthocyanin and spines.	Dwarf Leaf.
	Typical plant	Reduced size, reduced chlorophyll	Driver's Dwarf

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HAIRLESS SIAMESE CATS

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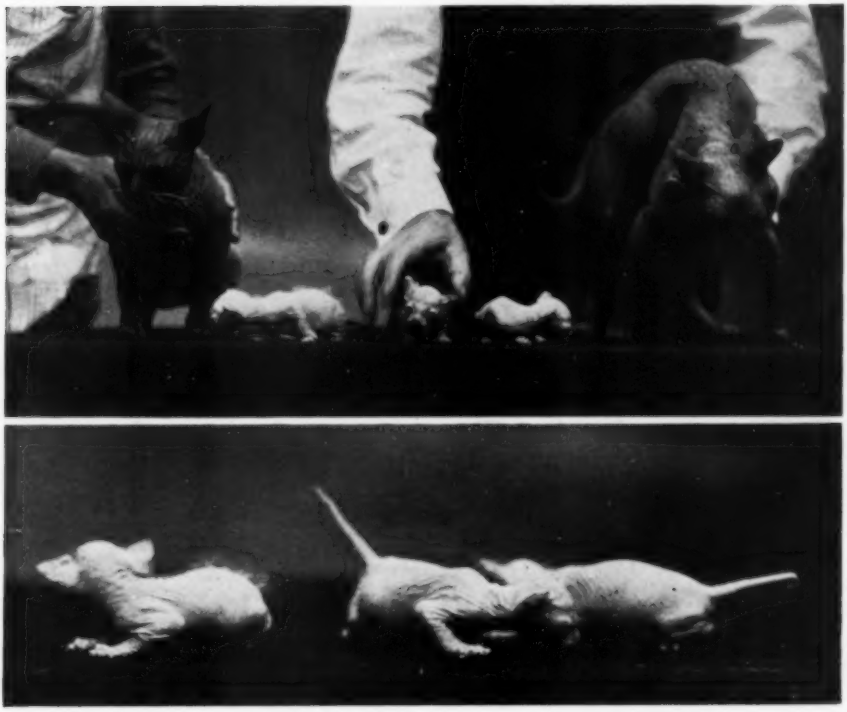
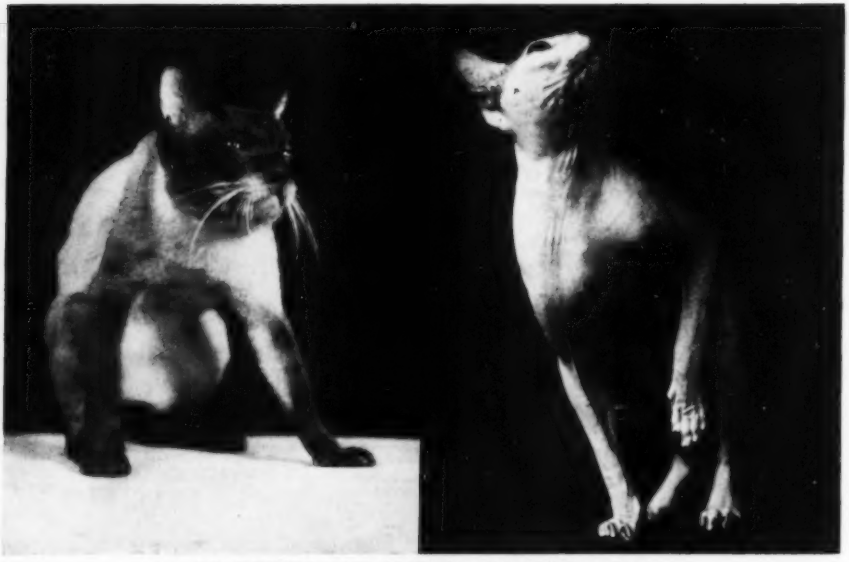


HAIRLESS SIAMESE KITTENS AND THEIR PARENTS
Figure 5

Two views of hairless Siamese kittens twelve hours old, and their parents. All of them are hairless though one has a thin coat of short hairs. Note the fur distinctly visible on one of the kittens. This is especially thick on the ears and in the axes of the limbs. It disappears in a few days, being followed a short time later by another transitory coat.

THE two accounts of "Nonesuch", the alleged cat-dog hybrid in the JOURNAL (March and September, 1937), have greatly interested the writer because he has had an opportunity to study a startingly similar variation in Siamese cats. The accompanying photographs show the appearance of the hairless cats, whose resemblance to "Nonesuch" is obvious. The origin and description of this hairless strain follows.

A pair of Siamese cats, perfect in type with normal hair and coloring, produced from time to time one or two hairless kittens in a litter consisting otherwise of normal kittens. From these periodically appearing hairless individuals we have been able to create a strain of hairless cats, which we believe to be entirely pure.



"CARRIER" AND NAKED SIAMESE CATS

Figure 6

On the left is a normally haired Siamese cat, which mated to a normal-haired male produced hairless offspring. She thus carries the recessive hairless gene. At right a mature hairless Siamese cat, the type of this recessive mutation. Note that the vibrissae ("whiskers") are normal. The whiskers of some hairless mammals are also affected.

If one mates one of the two individuals who have produced this mutation, with other normal Siamese cats, a hairless kitten has never been produced. Only the mating of the two individuals in question produces the mutation. The crossing of a hairless animal with other normal individuals has never produced a hairless cat.

We have mated two hairless cats, brother and sister; three hairless kittens were the result. With the exception of unforeseen circumstances which would have to be studied, the "hairless" can therefore be considered a type governed by the Mendelian law with hairlessness recessive to normal coat. Thus we find ourselves in possession of a strain, apparently already stable, which might be the origin of a distinct race, resuscitating the ancient race of so-called Mexican hairless cats, which is believed to be extinct.

It is imperative to mention that, though certain specimens are completely hairless, others have a slight down on their bodies. This down is subject to periodical changes, apparently closely connected with seasonal variations in temperature.

Strange as it may seem, the young ones which grow into hairless cats are not so at birth, but have a growth of hair, less dense, however, than normal. A transitory pelage in young hairless rats has also been reported.[2] The fact that the typical pattern of the Siamese cat is controlled in its development by temperature[1] may have a significance in this connection. This growth is most marked on the ventral surface and in the axils of the limbs. Between the tenth and fourteenth day after birth this juvenile hair has disappeared, and the "hairless skin" has become reality. The skin remains bald for several days and this is followed by another growth of hair. When the kitten has reached the age anywhere from eight to ten weeks it is covered with an abundant growth of

hair which gradually disappears, until at the age of six months the final stage of adult nakedness has been reached; either the skin is completely hairless, or covered with a slight down, subject to seasonal changes.

The fact that this mutation was observed in animals which have always lived in Paris, proves again that it is not always in special environments that one has to search for visible variations, and emphasizes again the random nature of spontaneous changes in inherited characters which appear to be one of the basic mechanisms of organic evolution.

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Genetics of Resistance to Bacterial Wilt in Maize

DURING 1931-33 bacterial wilt or Stewart's disease of maize, caused by *Phytomonas stewarti* (E.F.S.) Bergey *et al* [*Bacterium stewarti* E.F.S.], was more widespread than ever before known. None of the commercial early yellow varieties of sweet corn grown at that time was resistant, and losses often as high as 50 per cent in such varieties were encountered. Since resistant strains or varieties offer the only practical means of control for this disease, such losses led to the initiation of an extensive plant breeding program for the development of resistant, early maturing strains of sweet corn. The object of the investigations reported herein was to determine how resistance is inherited. The availability of this station of a large number of different, highly stable inbred lines of maize offered unusual opportunities for investigation of the problem. * * *

Many crosses were made between inbreds of various degrees of resistance and tested for dominance relations. In general, the crosses were approximately equal in resistance to that of the more resistant parent involved. A few of the crosses between inbreds intermediate in resistance, however, were more resistant than either of the parents. This was attributed to supplementary action of resistance factors.

Inheritance studies were chiefly confined to the analysis of the later generation progenies of two crosses: OSF, a very resistant inbred of dent corn, × WF a very susceptible inbred of flint corn, and OSF × W-134, a very susceptible inbred of early yellow sweet corn. Tests of the F_1 progeny showed that dominance of resistance was fairly complete.

Backcross progeny (F_1 × susceptible) of both crosses would readily be divided into four equal groups on the basis of resistance and susceptibility: Very resistant, moderately resistant, susceptible and very susceptible. It was assumed that these different degrees of resistance were due to the independent segregation of two supplementary factors, Sw_1 and Sw_2, completely dominant over their recessive allels, sw_1 and sw_2, respectively. Accordingly, the very resistant genotypes contain both Sw_1 and Sw_2, moderately resistant genotypes possess Sw_2 alone, and the very susceptible genotypes are double recessive, containing neither of the two dominant factors.

In certain of the backcross tests made under different environmental conditions, it was evident that each of the four groups was not a homogenous lot. Each could be subdivided into two groups, one being slightly higher in resistance than the other. This indicated that a third minor supplementary factor, Sw_3, was involved. Acording to the data this factor, when alone, produces a degree of resistance only slightly higher than that exhibited by the triple recessive types and when in combination with either or both Sw_1 or Sw_2 modifies their expression by slightly increasing resistance.

Results of F_2 tests and tests of F_2 and backcross families sustained the above factorial hypothesis. It was concluded, therefore, that at least three (two major and one minor) dominant, independently inherited, supplementary factors are involved in the inheritance of resistance to bacterial wilt in maize. The presence of all three factors either in heterozygous or homozygous dominant conditions (Sw_1 $sw_1Sw_2sw_2Sw_3sw_3$ or $Sw_1sw_1Sw_2sw_2Sw_3sw_3$) results in a high degree of resistance, whereas the triple recessive condition ($sw_1sw_1sw_2sw_2$ sw_3sw_3) results in a high degree of susceptibility. The various intermediate degrees may be explained by the presence of only one dominant factor or the different possible combinations of any two.

It was demonstrated that the parental combinations, red cob color and resistance, and white cob color and susceptibility, were more frequent in the backcross and F_2 progeny than the non-parental. This signifies that one of the factors for resistance is genetically linked with the P-gene for cob color. The frequency of the non-parental types indicates that the linkage is not very close. * * *

Endosperm characters such as yellow or white color and starchy or sugary texture seemed to assort independently of resistance.—From Introduction and Summary of "Genetics of Resistance to Bacterial Wilt in Maize." By E. J. WELLHAUSEN, *Iowa Agricultural Experiment Station Research Bulletin*. 224. Pp. 73-114. 13 illustrations. Oct., 1937.

SCIARA REYNOLDSI

A New Species which Hybridizes with *Sciara ocellaris* Comst.

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FOR several years a species of fungus fly which appears to be *Sciara ocellaris* Comstock, has been used in this laboratory for genetic and cytological studies. Several wild strains have been secured from various localities for this purpose. One strain of flies, sent by Dr. J. Paul Reynolds from Birmingham, Ala., appeared to be identical with our laboratory stocks, but was found, through breeding experiments and cytological study, to represent a distinct species. Subsequent observations have revealed external morphological distinctions between the two. Since the species are being used for hybridization studies as indicated in the accompanying paper, a brief taxonomic account will be given here.

The account is based not only on a comparison of laboratory strains of these two species, but also on a comparison of both of these with cotype specimens of *S. ocellaris* Comst. The latter comparison makes it clear that the species described here as *S. reynoldsi* is distinct from *S. ocellaris*. It also suggests, however, that the laboratory material which we have called ocellaris may likewise belong to a distinct species. If this should prove to be the case it is probable that all three species will hybridize. The present account is made possible by the kindness of Prof. O. A. Johannsen who has prepared and loaned a wing mount from one of the two cotype specimens of *S. ocellaris* Comst., has compared our material with these cotypes and has verified our observation that *S. reynoldsi* is a distinct species.

Characteristics of *S. ocellaris*

The following description of *S. ocellaris* Comstock is taken from the review by Johannsen.* It should be noted in this connection that the two present species belong to the subgenus *Neosciara* Pettey.

Sciara ocellaris Comstock

Rept. of Comm. of Agr. 203. 1882.

Male. Length 1.5 mm. Head black, antennae dark brown, basal joint light yellowish brown; pronotum light yellowish-brown; mesonotum yellowish brown in the center and darker at the edges; scutellum dusky brown; metathorax dark brown, almost black; abdomen with caudal portion of the segments blackish, cephalic portions yellowish brown; clasper lighter brown. Poisers, with knob blackish, and base light brown. Tibiae and tarsi dusky brown; femora lighter; coxae still lighter.

This description was accompanied by a figure of a wing of a type specimen (Johannsen 1912, Fig. 265), in which most of the details of wing venation may be observed. A photograph taken from the cotype wing kindly loaned by Prof. Johannsen is represented in the accompanying Figure *7B*. These two wings appear to agree in all essentials. For comparison with our material the following characteristics of venation should be noted (see Figure *7A* for explanation of terminology). Since the humeral cross vein is very faint, and the shoulder of the petiole of the radius just below it is conspicuous, in these species, the latter rather than the former is used here as a base for measurements.

Vein Cu_1 is 5.5 times as long as petiole of Cu, and conspicuously arched; section of the

*JOHANNSEN, O. A. 1912. The fungus gnats of North America. Part IV. Bulletin, Maine Agr. Exp. Sta. No. 200, pp. 57-146.

media lying between the cubitus and the *R-M* cross vein is 1.4 times as long as petiole of cubitus, 2/5 as long as the next section of media (*M* in Figure 7*A*), 1/4 as long as *R-M* plus R_s, and twice as long as the *R-M* cross vein; second segment of petiole of radius is 1.5 times length of R_1; distance between apices of Cu_2 and Cu_1 equal to that between apices of Cu_1 and M_2; veins Cu_1 and Cu_2 parallel for a distance but little more than length of petiole of *Cu*; distance from apex of costal vein to apex of M_1 is 1/3 - 1/2 length of apical segment of costal vein.

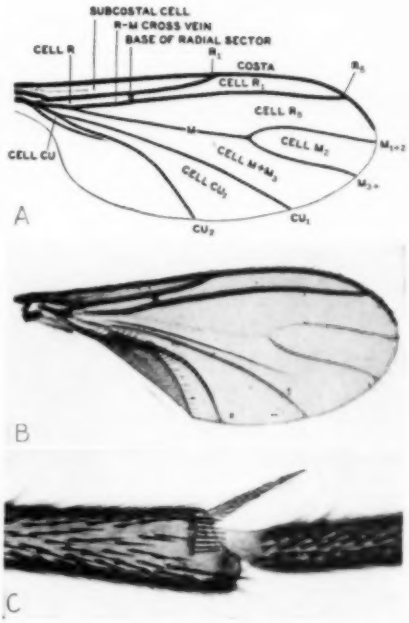
Laboratory Strains of *S. ocellaris*

Laboratory strains derived from wild specimens secured at Birmingham, Ala., by Dr. J. P. Reynolds, and at Guilford, N. C., by Mr. T. L. Reynolds, conform in general characteristics to the description quoted above for *S. ocellaris*. Likewise they agree for the most part in wing venation, as may be seen by comparing Figure 7*B* of the present paper with Figure 8 *A* and *B* of the accompanying paper by Metz and Lawrence. It should be observed, however, that the segment of the media vein between the cubitus and the *R-M* cross vein is considerably longer in the cotype of ocellaris (Figure 7*B*) and in Johannsen's figure 265 than in any of our material. This suggests that our material may represent a distinct species or variety; but the evidence is not sufficient to establish such a distinction at present. The following measurements have been taken from our laboratory specimens. Male and female:

Vein Cu_1 is 4-7 times as long as petiole of cubitus; section of the media lying between the cubitus and the *R-M* cross vein is 1-1.3 times as long as petiole of cubitus, 1/3 (or less) as long as the next section of the media (*M* in Figure 7*A*), 1/5 as long as *R-M* plus R_s, and equal to *R-M*; second segment of petiole of radius 1.5-1.9 length of R_1; distance between apices of Cu_2 and Cu_1 equal to or less than distance between apex of Cu_1 and apex of M_2; veins Cu_1 and Cu_2 not parallel at all or only parallel for a distance but little more than the length of petiole of *Cu*; distance from apex of costal vein to apex of M_1 about 2/5 as long as apical segment of costal vein.

Sciara reynoldsi n. sp.

Males and females are similar in size and general color characteristics to *S. ocellaris*, conforming to the description cited above for the latter. They may be distinguished from ocellaris, however, by the shape of cell Cu_1, the shape of vein Cu_1, the position of the base of the radial sector, the length of the costal vein and other characters noted below.



SPECIES—DIFFERENTIATING CHARACTERS

Figure 7

A—Wing of *Sciara reynoldsi* female made by tracing with ink on a photograph and then bleaching the photograph. From a wild specimen. *Cu*, cubitus; *M*, media; *R*, radius. Terminology after Johannsen. *B*—Photograph of wing from a male cotype specimen of *Sciara ocellaris* Comstock. From a preparation kindly loaned by Professor O. A. Johannsen from the Cornell University collection. 50×. *C*—Apex of the tibia from front leg of male *Sciara ocellaris* (laboratory stock 1917) showing comb and spur. 300×. In reynoldsi the comb is shorter relative to the spur.

Female. Vein Cu_1 is ten times as long as the petiole of the cubitus, and not conspicuously arched; section of the media lying between the cubitus and the *R-M* cross vein is about 1/4 as long as the next section of the

media (*M* in Figure 7*A*), about 1/7 as long as *R-M* plus R_s, and about 2/3 as long as the *R-M* cross vein; second segment of petiole of radius 1.1-1.5 length of R_1; distance between apex of Cu_1 and Cu_2 greater than distance between apex of Cu_1 and apex of M_3; veins Cu_1 and Cu_2 parallel or almost parallel for a distance equal to about three times length of petiole of cubitus; distance from apex of costal vein to apex of M_1 is 1/4 length of apical segment of costal vein.

Male. Wing venation similar to female, but proportions more variable and not always so distinct from those of ocellaris. Most easily distinguished by characteristics of cell Cu_1, length of petiole of cubitus and distance between apices of costal vein and M_1. No difference has been detected in the hypopygia of the two species.

This species has been secured in Birmingham, Ala. (J. P. Reynolds), Guilford, N. C. (T. L. Reynolds), and Raleigh, N. C. (C. B. Davidheiser). Type and cotype specimens are deposited in the Cornell University collection.

In most cases examined, the two species are easily distinguished by the position of the base of the radial sector, which determines the relative proportions of segments two and three of the radius. In ocellaris the second segment is much longer than the third in all of our material; in reynoldsi it is usually only slightly longer, but there is more variability here and in some cases the proportions are not significantly different from those in ocellaris. There are other characteristics distinguishing the species; but those detected thus far are difficult to express accurately. For example, the length of the comb in relation to that of the spur near the apex of the front tibia (Figure 7*C*) averages longer in ocellaris than in reynoldsi; the apical segment of the ovipositor is longer in ocellaris than reynoldsi, and cell *Cu* is more prominent and wider in ocellaris than in reynoldsi.

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Statistical Mapping

A JOINT publication by the American Geographic Society and the Population Association of America presents a symposium of mapping which was a feature of the October, 1937, meeting of the Population Association. Various methods of presenting statistical data on maps are discussed and the mechanics of shading, cross-hatching and dotting are gone into in considerable detail. The optics of various distributions of black and white are discussed by Dr. Lloyd A. Jones of the Eastman Kodak Company, and by Mr. Leonard Stone of the American Telephone and Telegraph Company. It is shown that the pattern of distribution of black and white determines the greyness to a greater extent than percentage of black and white. Much of this material should be of great value to all who feel a compulsion to prepare graphs and charts. "Statistical Mapping" may be obtained from the American Geographic Society, Broadway at 156th St., New York City. Price 50c.

PRELIMINARY OBSERVATIONS ON SCIARA HYBRIDS

Between *S. ocellaris* and *S. reynoldsi* (Diptera)

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As noted in the accompanying paper, a new species of Sciara (*S. reynoldsi*) has been secured which hybridizes with the closely related species, *S. ocellaris* Comst. In general appearance the two species are so nearly identical that their distinctness was only noted after it was found that many of the cross matings between them failed to give offspring and that their salivary gland chromosomes differ in pattern. The results of preliminary hybridization studies and comparison of chromosomes are given below. Review of the literature and comparison with conditions in other organisms will be deferred until more detailed results are secured.

Before considering conditions in the hybrids it is necessary to recall some of the peculiarities found regularly in ordinary reproduction in Sciara. Several species of Sciara regularly give "unisexual" families[2,5]. Some females are male-producers and others female-producers. Several other species regularly give bisexual families (but not 1:1 sex ratios). Still other species possess strains of both types. *S. ocellaris* is one of the latter species, while *S. reynoldsi*, so far as known, gives only bisexual families. In the present experiments most of the *S. ocellaris* flies used were from a strain giving "unisexual" families. Since the sex of the family is determined by the mother most of the hybrid families are "unisexual," i.e., each consists mainly or entirely of males or of females. When the family is not strictly unisexual a few individuals of the opposite sex are referred to as "exceptionals." Thus a few "exceptional" males may appear in a female progeny, or females in a male progeny.

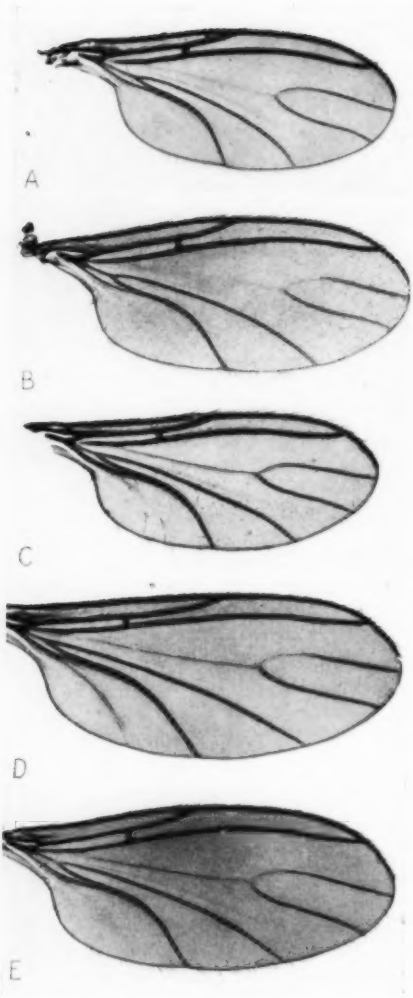
Another peculiarity requiring notice here is the fact that in the present material the male transmits only the chromosomes and genes received from his mother[3,4,9,10]. Consequently a hybrid male is genetically "pure" *S. ocellaris* where, as in the present case, this species is used as the female parent.

Hybridization Results

1. No offspring have thus far been secured from matings of *S. reynoldsi* ♀ × *S. ocellaris* ♂, although 45 pair matings of this type have been made (Table I).

2. *S. ocellaris* ♀ × *S. reynoldsi* ♂ give vigorous, viable offspring in relatively large numbers. Out of 162 pair matings 71 gave offspring, as shown in Table I. Full counts were made in 10 cases, with the following results, expressed as female : male ratios: 39:0, 98:0, 72:0, 0:126, 0:68, 0:75, 0:80, 0:171, 13:80, 11:89. The last two included three gynandromorphs. No gynandromorphs were recorded in the others, but since these families were the first hybrid families examined gynandromorphs may have been overlooked in them. Comparison of these counts with counts from pair matings of pure ocellaris, using females from the same cultures as those used in the above crosses, shows that the hybrid families are approximately as large as the others. The families in both cases are rather small, due to poor conditions at the time, but apparently fertility is good in the successful hybrid matings. Why so many are not successful is thus far unknown.

3. Apparently all hybrid females are



WINGS OF PARENT SPECIES AND OF HYBRID

Figure 8

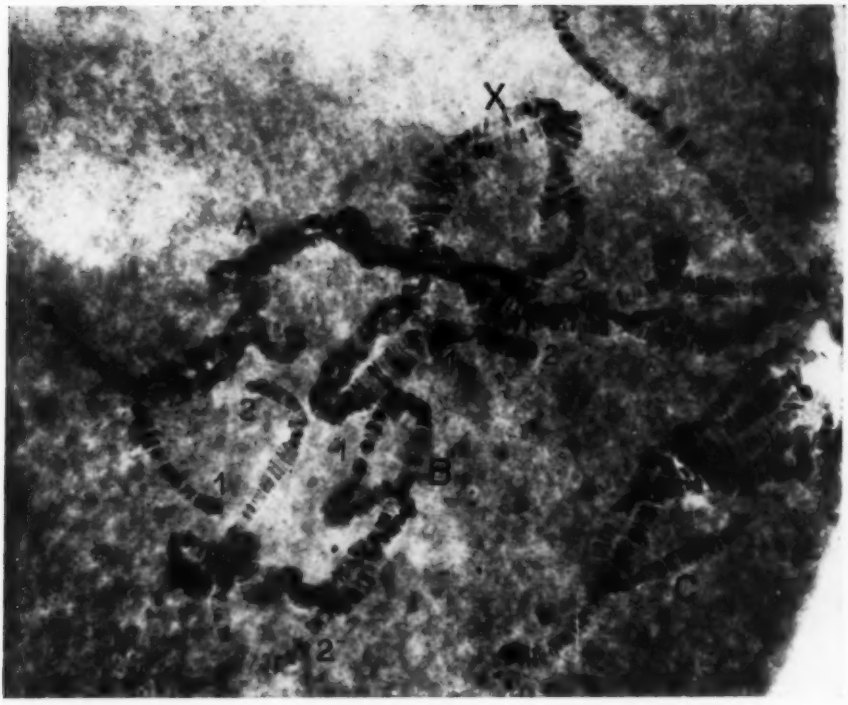
Photographs of wings of pure parental species, 25×: *A*—*S. ocellaris* ♂, *B*—*S. ocellaris* ♀; *C*—*S. reynoldsi* ♂, *D*—*S. reynoldsi* ♀; *E*—Hybrid ♀ from *ocellaris* ♀ × *reynoldsi* ♂. The hybrids tend to be intermediate between the parents in the characters which differentiate the two species.

sterile. As shown in Table I, fifty matings of such females all failed to give offspring. Twenty-two of these were backcrosses (12 to reynoldsi and 10 to ocellaris) and 28 were matings to hybrid males.

4. Hybrid males, on the other hand, are not all sterile. Thirty-seven matings of such males to reynoldsi females failed to give offspring, as shown in Table I, but among 10 similar matings to ocellaris females 8 were fertile, as shown in Tables I and II.

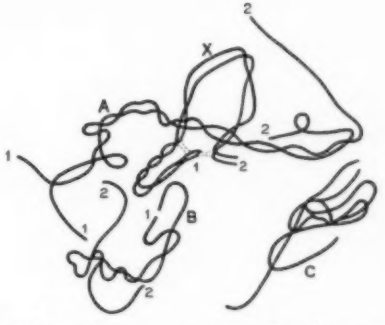
5. Table II represents the individual records of the tests of hybrid males × ocellaris females. The first is a pair mating; the other 9 represent matings in each of which several males were put with three or four females. The fact that offspring were obtained in 8 out of the 10 matings indicates that many of the hybrid males were fertile. The hybrid males used in those eight fertile matings came from five different cultures, indicating that fertile males appear commonly in this type of cross and do not represent special genetic combinations which appear only in the offspring from certain individual flies. Further tests are being made to determine the degree of fertility of hybrid males.

6. Many of the hybrids are gynandromorphs, representing various types of mosiacs of male and female parts. These will be treated more fully elsewhere, but a few points call for comment here. In nine individuals of this type the gonads were found to be unlike — one a testis, the other an ovary. This fact has an important bearing on the problem of sex determination in Sciara, as will be shown in another paper (Metz, in press), for it does not agree with findings in *Sciara coprophila*, in which the gonads of gynandromorphs were consistently found to be alike by Schmuck and by DuBois[1]. Three flies (from yellow mothers) which were yellow males in external appearance had one ovary and one testis each, and a fourth had two ovaries. These flies had normal male internal accessory genetalia and were in no way distinguishable externally from normal yellow males.



SALIVARY GLAND CHROMOSOMES OF OCELLARIS × REYNOLDSI HYBRID

Figure 9

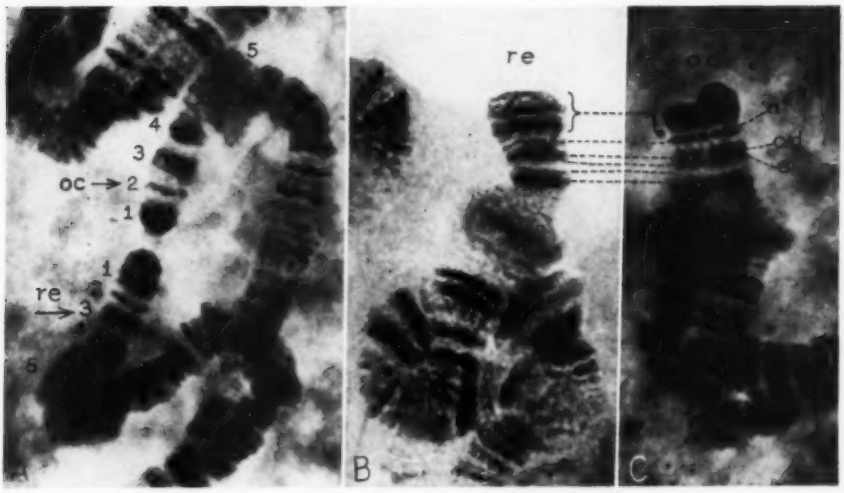


Photograph (562×) of entire chromosome group in salivary gland cell of hybrid from *Sciara ocellaris* ♀ × *S. reynoldsi* ♂, showing the paired association but only partial synaptic fusion of corresponding chromosomes. From a permanent aceto-carmine smear preparation. The group consists of four pairs of chromosomes (see diagram at right); one long pair (*A*) and two short pairs (*B* and *C*) of autosomes, and one pair of X-chromosomes (*X*). This figure should be compared with the corresponding photographs of pure *S. ocellaris* shown in an earlier paper in this JOURNAL (May, 1935, Frontispiece and Figure 2). The ends of the chromosomes are numbered to correspond to those in the earlier figure. Very little actual fusion of homologous parts is seen in any of the autosomes, but two fused regions are present in the *X*. The latter chromosome is shown at higher magnification in Figure 10, and end 1 of chromosome *B* is similarly shown in Figure 11*A*. The diagram at right shows positions of the four pairs of chromosomes (*A*, *B*, *C* and *X*) and indicates roughly the paired association of corresponding chromosomes. The association is close in the *X* pair and the *A* pair, but very loose in pairs *B* and *C*. The latter pair forms a confused tangle, part of which is broken off at the right, so no attempt is made to represent it accurately.

X-CHROMOSOME PAIRING

Figure 10

Photograph at higher magnification (1700×) of the X-chromosome pair shown in Figure 9. This chromosome pair exhibits two loops which superficially resemble inversion figures, as shown diagrammatically in the insert. But they are not due to inversions; they are due to normal duplications which appear regularly in *S. ocellaris*, as shown in Figure 13 and in the earlier figures already referred to. Duplications of somewhat the same kind are also present in the *X* of *S. reynoldsi*. The chromosomes of the two species are very similar in pattern throughout much of their length, as may be seen in this photograph. *A*, *B* and *C* indicate regions in which small differences appear. The letters *a*, *b*, *c* and *d* in the upper part of the figure indicate corresponding bands in a region where fusion has not occurred. Numbers 1 and 2 designate end 1 and end 2 of the chromosome (see Figure 13).



FINE STRUCTURE OF CHROMOSOME B

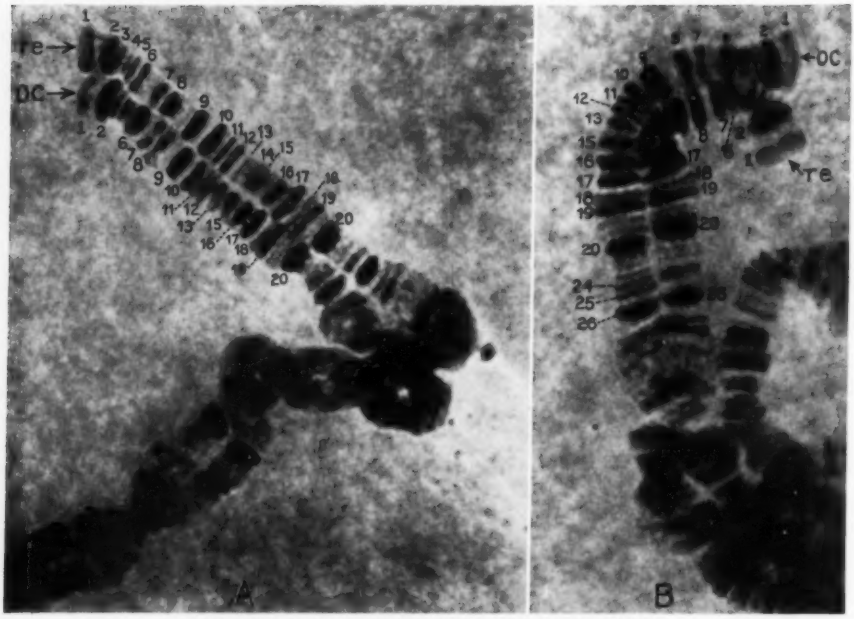
Figure 11

A—Photograph of end 1 of chromosome *B* in the hybrid (a higher magnification of part of Figure 9); and the same of the two pure species, *reynoldsi* (*B*) and *ocellaris* (*C*)—all 1700×. In the hybrid the two corresponding chromosomes are attached at their tips—a characterisitc seen in many other cells also (*oc* designates ocellaris; *re* reynoldsi). This chromosome shows good examples of the small differences in corresponding regions. Note that the general pattern is similar, as indicated by corresponding numbers (1, 2, 3, 4, 5) but that the structural details differ (e.g. in regions 1 and 3). Compare also with earlier photographs in this JOURNAL (May, 1935, Figures 5 and 6) showing this region in *S. ocellaris*. (In one homologue of the ocellaris chromosome pair there is a terminal deficiency or a small addition.) Small regions which apparently correspond in a general way in the chromosomes of these species (*B*, *C*) are connected by dotted lines. Note that the characteristic expanded or "puffed" region is present in corresponding position in both chromosomes (shown also in *A*).

7. Many other hybrids were dissected for examination of their internal genitalia. Abnormal gonads were found in most cases. Ovaries usually contained only small numbers of eggs, but these appeared normal on superficial examination. Testes were usually small and shrunken, but contained sperms.

8. In many of the original crosses a sex-linked mutant character, yellow body color, in *S. ocellaris* was used. This served the double purpose of "marking" the ocellaris *X*-chromosome as a check against contamination or non-virginity of females, and of revealing distinctly the distribution of male and female parts in the gynandromorphs. Yellow ocellaris females were mated to wild-type reynoldsi males. From such matings the daughters should all be wild-type (symbol +) and the sons all yellow (symbol y); and correspondingly in gynandromorphs the female and male parts should be wild-type and yellow respectively. This expectation was verified (Table III). As shown by this latter table seven kinds of families were secured. The mosaics which characterize the last four types, are presumably due to hybridization. Since 13 of the 15 families giving "exceptional" males or females include mosaics, it seems probable that the production of mosaics is associated with the production of "exceptional" individuals. This feature may likewise have particular interest in connection with the problem of sex determination in Sciara, but not enough is known about it to warrant discussion at present.

9. As noted above, the males here transmit only the chromosomes received



ASSOCIATION OF HYBRID CHROMOSOMES

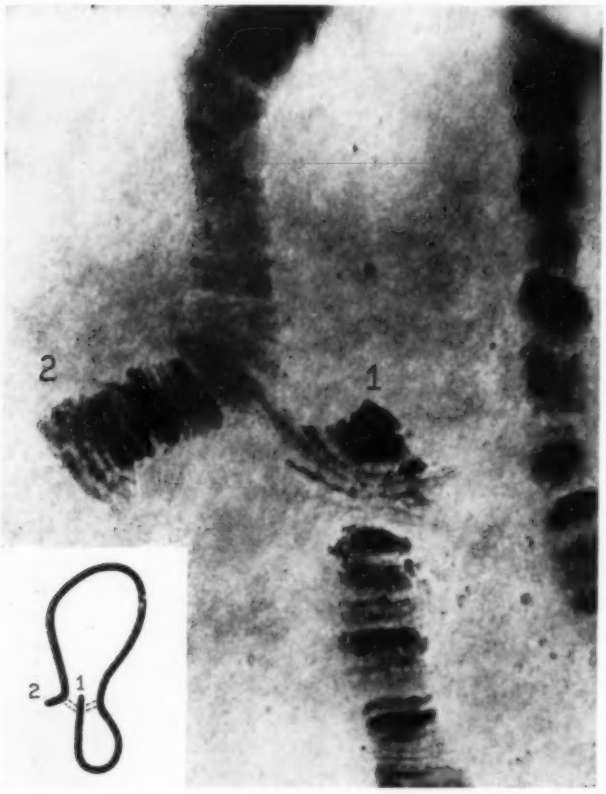
Figure 12

Two photographs showing end 1 of pair *A* in a hybrid from *S. ocellaris* ♀ × *S. reynoldsi* ♂. From two salivary gland cells of one specimen; permanent aceto-carmine preparation, 1700×. Note the intimate pairing of corresponding regions, but very little actual fusion. Compiete fusion is conspicuous only in the region below that marked 26 in *B*. Bands or short regions which are similar in the two species are given corresponding numbers, using the same designations as in previous figures of chromosome *A* in the JOURNAL OF HEREDITY (May, 1935, Figures 4 and 5). Note the small differences between the two species at regions 1, 10, 12 14 in *A*. A conspicuous difference is seen also at 6; but in some specimens, or strains, of ocellaris the structure at 6 is like that in reynoldsi (see Metz, 1937, Figures 6, 7, 8, 17, 19, 20). *oc*, ocellaris, *re*, reynoldsi.

from their mothers; consequently, the present hybrid males all behave genetically as if they were pure *S. ocellaris*. This fact alone presumably does not account for their fertility, however, because if it did the hybrid males should all be fully fertile; likewise it might be expected that the females would be partially fertile for each should produce some eggs retaining only maternal chromosomes after maturation.

10. It seems significant that both the original cross and backcross matings are successful only when ocellaris is used as the female parent. Since the hybrid sperms transmit only ocellaris chromosomes this suggests that the ocellaris egg, or its cytoplasm, is compatible with the chromosomes, or the sperms carrying the chromosomes, of either species, but that the reynoldsi egg is only compatible with reynoldsi chromosomes or sperms.

11. The hybrids tend to be intermediate between the two parents in respect to the taxonomic characters used to distinguish the species, although they are not uniformly intermediate as indicated by the wing photographs in Figure 8. Wings of two hybrid females from separate matings were mounted and examined in detail. These appear to be just alike. In them the petiole of the cubitus is intermediate while the shape of cell Cu_1 is more like that of ocellaris.



"REPEATS" CAUSE "FIGURE 8" SYNAPSIS

Figure 13

Normal *X*-chromosome pair of *S. ocellaris*. Photograph showing the duplications ("repeats") which cause this pair to appear usually in the form of a figure 8 in salivary gland cells (see insert and Figures 9 and 10). The duplications result in lateral attachments connecting bands near end 1 with bands near end *2* at the left) and with bands lying about 1/3 the distance from end 1 to end *2* at the right).

The position of the apex of the costal vein is somewhat intermediate, but distinctly more like that of ocellaris than reynoldsi, and similarly the position of the base of the radial sector resembles that in ocellaris. The evidence indicates, as would be expected, that the differences are due to numerous genic differences between the two species.

12. The ordinary metaphase chromosome groups of the two species are probably alike, each consisting of three similar pairs of rod-like chromosomes and one pair of V's (See Frontispiece, JOUR. HERED. May, 1935). The "limited" chromosomes (limited to the germline) found in other species of Sciara[9,5] are not found in the present two species.

13. In the salivary glands of hybrids the chromosomes are associated in symmetrical pairs, but complete synapsis or fusion is found in only a few short regions, as shown by the accompanying photographs. A more detailed account will be presented later, but two features of interest should be noted here.

(a) One is the apparent absence of inversion or translocation configurations (see Figure 9). None of the loops or crosses characteristic of such figures has been found. The significance of this fact is not yet clear. It may merely mean that the synaptic attraction of homologous parts is not so strong here as in Drosophila, although this seems doubtful, for in general synapsis is intimate in these species and often is not even interfered with by small deficiencies[8].

(b) The other is the high frequency of small differences in corresponding chromosomal regions. Numerous regions which are obviously similar in general characteristics, and which are associated or "paired," differ in respect to details of structure and in number of small chromatic bands, indicating that many very small chromosomal changes

have occurred in the course of the recent evolution of these species. Some of these differences are shown in the photographs in Figures 10-12.

AUTHOR'S NOTE: An interesting structural difference of the type just mentioned is found in chromosome *B* in the region *cd* as shown in Figure 11 *A, B, C*. The structure of this region in the ocellaris chromosome has been described in detail in an earlier paper in the JOURNAL OF HEREDITY,[7] and the lettering in the present figure corresponds to that used before. In ocellaris the two bands *cd* together usually form one row of large block-like granules as shown in *C*, whereas in reynoldsi the two corresponding (homologous?) bands are distinct, much finer in structure, and have never been found to form the block-like granules. This suggests that the structural differences reflect qualitative differences in homologous regions or loci in the two species.

The present Figure 11*C* also shows the honeycomb structure in the region *a-cd-e* represented in Figure 4*A* and 5*A* of the earlier paper.[7] Figure 6 in the earlier paper was likewise designed to show this feature, but the finer details visible in the photograph were lost in reproduction. Criticisms of our "honeycomb" interpretation[8a] by other observers will be considered in another paper where evidence will be given indicating that what these observers describe as visible "chromonemata" cannot be true chromonemata, also that the different observers refer to different things as "chromonemata."

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TABLE I. Tests of S. ocellaris X S. reynoldsi and of their F_1 hybrids.

Type of Mating	No. of Cultures	No. of Fertile Cultures
reyn.♀ X ocell.♂	45	0
ocell.♀ X reyn.♂	162	71
Hyb.♀ X reyn.♂	12	0
Hyb.♀ X ocell.♂	10	0
Hyb.♀ X Hyb.♂	28	0
reyn.♀ X Hyb.♂	37	0*
ocell.♀ X Hyb.♂	10	0

*1 larva which did not mature was found in this culture.

TABLE II. Tests of fertility of hybrid males from S. ocellaris female X S. reynoldsi male backcrossed to ocellaris females. Each record represents one mating, and in all except the first the males were put with three or four females. The symbol + indicates that some offspring were secured and - indicates that no offspring were secured.

Culture Number	Number of males tested	Result
800	1	-
936	4	-
937	7	+
938	10	+
939	3	+(few)
940	9	+
966	11	+
969	9	+
970	4	+
971	9	+

TABLE III. Types of hybrid families secured from yellow ocellaris females X wild-type reynoldsi males. The symbol Y designates yellow, and + designates wild-type.

Kinds of flies in F_1	Number of families.
y♂ only	22
+♀ only	10
y♂ and +♀	2
y♂ and mosaics	2
+♀ and mosaics	6
y♂, +♀, and mosaics	15
mosaics only	3
	60

A TETRAPLOID ZINNIA

A COLCHICINE INDUCED GIANT

Figure 14

The growing point of the zinnia on the left was treated as a seedling with colchicine solution. Its pollen grains are uniformly about twice the volume of the pollen grains of control plants of the same parentage, of which one is shown at the right. This indicates that chromosome doubling has taken place.

THAT the Colchicine method of doubling chromosomes will be very extensively tested in practical plant breeding is strongly suggested by the flood of inquiries which followed the articles published in the December and January issues of the JOURNAL. Perhaps the first successful use of Colchicine in commercial plant breeding is recorded in a note from Mr. Gordon Morrison of the Ferry-Morse Seed Company announcing the production of a tetraploid zinnia by colchicine treatment. The accompanying photograph shows the plant produced by treatment of the terminal bud with colchicine as compared with a normal plant of the same variety. The method used is thus described by Mr. Morrison:

We have used the size of the pollen grains

as our criterion in determining that tetraploidy has been induced in this instance. Furthermore, this plant has distinctly the largest flowers of any of the zinnia plants in the test.

We used the so-called "drop method" of applying colchicine to newly emerged seedlings. Most of those given a highly concentrated dosage soon become badly stunted and did not develop beyond the cotyledon stage. Practically all those which were given a relatively weak dosage became somewhat stunted and gradually resumed normal growth. In fact, I examined more than forty treated individuals before I finally found one with uniformly and distinctly large pollen grains. The pollen grains of this plant are twice as large as those of the other individuals. Untreated zinnias were also used as checks. An eyepiece micrometer (10 mm=100 divisions) was used to compare the size of the pollen grains. Of more than 40 treated and untreated plants, judged as normal, none yielded pollen grains with a diameter greater than 10 divisions at × 400 magnification. The average diameter was about 9.5 divisions. The diameter of the tetraploid pollen grains averaged about 12.0 divisions, but varied from 11.0 to 12.5. There were some normal sized grains in one of the florets.

The enclosed print shows the treated plant with large pollen and a treated plant with normal sized pollen. These treated plants are rather rough, scrawny and unattractive due to the severity of the colchicine treatment. However, they are double dahlia flowered individuals with good ancestry. The tetraploid should eventually give us a fine giant flowered strain of Double Dahlia Flowered Zinnia, variety Oriole.

The same technique is being used with many other decorative flowers, and on vegetables by Mr. Morrison and he is very hopeful that other genera will yield giant varieties of economic importance.

Undoubtedly many very useful variations will be obtained by the colchicine technique, but we must not expect that it will be uniformly successful, and some little time must elapse before enough experience has been accumulated to indicate just where the production of forms with double chromosomes will be of economic value. Mr. Morrison also writes that an effort is being made to produce fertile "double diploids" from sterile first generation hybrids. Success in this is without doubt one of the most spectacular possibilities which colchicine technique offers, and we look forward hopefully to later reports. Even though only a small proportion of sterile hybrids should prove susceptible to such treatment, the method might have revolutionary results.

Colchicine A Dangerous Drug

Colchicine is being so widely used in experiments that a repeated word of warning regarding its extremely poisonous nature may not be amiss. Dr. R. B. Nebel reviewed the literature on this drug at some length and states that great care should be exercised not to let even dilute solutions of the drug touch the skin. Should this occur it should be washed off immediately. The writer had a painful and alarming experience during the winter, when he got a very small quantity of dust of the amorphus colchicine into his eye. Some hours later a violent inflamation set in which resulted in virtual blindness for over two weeks. No permanent harm resulted, and the eye does not seem to be a tetraploid at this writing. Nevertheless the involuntary experiment is one he would not like to repeat or to have others undertake.

Considerable work is being done on cytological studies of the effect of colchicine on the chromosomes and on the rest of the dividing cells. A detailed report of some of this work is scheduled for an early issue of the JOURNAL.—ED.

ANOMALIES AND CAST DETERMINATION IN ANTS

P. W. WHITING
University of Pennsylvania

IN a manuscript completed just before his death, Professor William Morton Wheeler has made a final and noteworthy contribution to our knowledge of ants. The material has been published posthumously in an attractive little volume of 95 pages.* The 18 figures include photographs of the insects, their nests and nesting sites, as well as drawings of normal and aberrant types. The discussion centers about a remarkable colony of the fungus ant *Acromyrmex octospinosus* Reich, collected by Dr. Neal Albert Weber in Trinidad and studied by him in a laboratory observation colony from May 5 to August 7, 1935. The entire personnel of the colony, including 8,012 normal and 164 aberrant individuals, was preserved in alcohol along with the fungus garden and turned over to Professor Wheeler for study. The book contains a detailed description of these specimens and a digest of Dr. Weber's observations.

The emphasis throughout is placed on the problem of caste determination, a moot question for many years. Taxonomic notes on the various subspecies of *octospinosus* are given. Phylogeny of the different groups of ants, especially of the fungus-eating Attini, is discussed along with the relationship of ants to wasps and bees. There is a thorough treatment of sex and caste mosaics as reported in the literature and a very useful classification of non-mosaic anomalies which are grouped as being derived by modification from the reproductive female, the worker or the soldier. Seventeen of these types are nonparasitogenic. The other nine are caused by parasites,—Mermis, Chalcidoid wasps and Staphylinid beetles. A bibliography is appended which should prove very valuable to the student who wishes to delve more deeply into the subject.

It is now generally agreed that the males of ants develop parthenogenetically from unfertilized eggs, so that sex may be said to be determined genetically; but what determines the various female castes? Is it blastogenic (genetic) or trophogenic (environmental)? Wheeler states "that the controversy concerning the determination of the castes in these insects has persisted with little change for many years. This is shown by the attitudes of the two very eminent myrmecologists, Emery and Forel. Although both were thoroughly conversant with all the relevant facts established during their lifetimes, Emery nevertheless remained an intransigent trophogenist throughout his career, and Forel, though he wrote less on the subject, was as thoroughly convinced that the castes were determined in the egg. During the past thirty years I have remained 'on the fence' in this controversy, with an increasing inclination to drop off on the blastogenic side." It would be impossible in the space of this review to give an adequate summary of the evidence bearing on caste determination contained in this volume. It includes the comparative morphology of the normal castes and of the parasitogetic anomalies in different species, food and care of the young and the intimate life within the nest, as well as a detailed discussion of the so-called mosaics already described in the literature and the remarkable series here published for the first time. The student of genetics will be especially in-

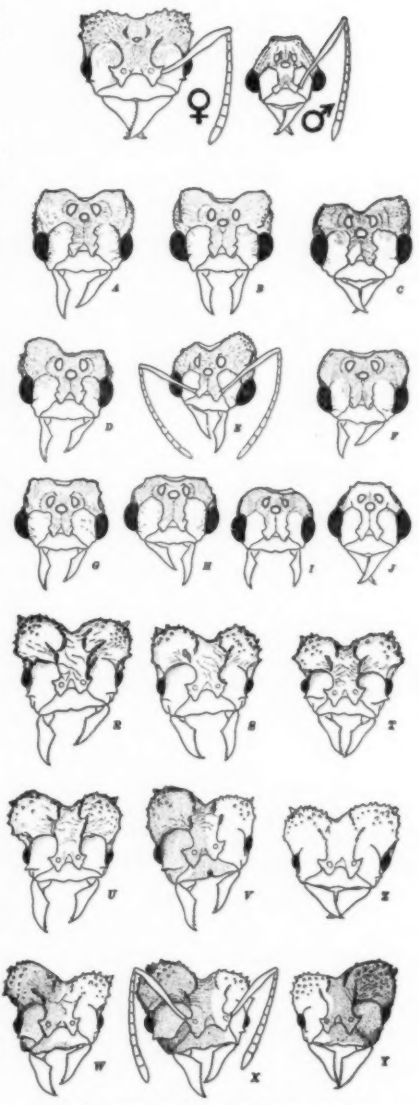
*WHEELER, WILLIAM MORTON, with a foreword by THOMAS BARBOUR, *Mosaics and Other Anomalies Among Ants*. Pp. 95, 2 pl., 18 figs. $2.00. Harvard University Press: Cambridge, Mass. 1937.

terested in the nature and possible cause of origin of these last mentioned aberrant types.

Sex-Intergrades

Professor Wheeler holds that just as a sex-mosaic indicates genetic difference between normal males and females, so also a caste-mosaic indicates that the differences between the various female castes (workers, soldiers, and sexual females) are determined genetically. On this basis the blastogenic or genetic view is favored for caste determination in ants, although it is agreed that in bees and wasps the separation of queen from workers is a matter of nutrition By reason of his studies of mosaics in the parasitic wasp *Habrobracon*, the reviewer would like to venture an alternative suggestion in regard to many of the so-called mosaics of ants. In true mosaics the two genetically different parts of the body are distributed more or less at random. In a gynandromorph, for example, the male regions may be limited to anterior or to posterior half, to right or to left side, or there may be a male spot or island in a female head or abdomen. In the so-called mosaics of ants, however, the anomaly tends to be limited to the head and this limitation is, according to Professor Wheeler, characteristic of many of the 61 "gynandromorphs" described by other authors as well as the numerous "mosaics" presented for the first time in the volume under review. It may be suggested, therefore, that we are here dealing not with sex and caste mosaics but with sex and caste intergrades of another sort, namely, intersexes and intercastes.

According to Goldschmidt, whose work on the gypsy moth, *Lymantria*, may be especially cited in this connection, an intersex begins development as one sex but later at a specific turning-point shifts so that organs subsequently developed are according to the pattern of the opposite sex. An intersex is then not a mosaic in the genetic sense, although it may suggest one phenotypically. The line separating the sexually different parts is drawn not at random



MOSAICS OR INTERGRADES?

Figure 15

Normal female and male of *Acromyrmex* and eighteen anomalies. *A-J* are either gynandromorphs or intersexual males. *R-Y* are female-worker intergrades, either caste mosaics or intercastes. *Z*, an intergrade of media and major worker, has coloration normal for workers. From Wheeler's Figs. 7-8, 11.

over the body surface but at a definite time in embryonic succession. Thus the superficial details may be in pattern characteristic of the sex opposite to that shown in more fundamental structures. The earlier the turning-point the greater the degree of intersexuality, so that a highly intersexual male may externally resemble a female and *vice-versa*. Intersexuality may be caused genetically by race-crossing as in *Lymantria*, or it may result from trophogenic or other environmental influences.

In addition to the *Acromyrmex* colony, Dr. Weber also collected a second colony, much larger in size, of a large Cryptocerine ant, *Cephalotes atratus quadridens* DeGeer. Although detailed description of these specimens was being reserved for later treatment, Professor Wheeler states that it contained more than 4000 "gynandromorphs" and that "in fully 95 per cent of them the male component is confined to the head." These then may be regarded as female intersexes unless, indeed, further evidence indicates that they are also intercastes, starting development as workers and transgressing both caste and sex lines.

The 8,012 normal individuals of the *Acromyrmex* colony include eleven females with wings removed (dealated) and therefore mated. These are regarded as the mothers of the other normal members of the colony, — 660 males (winged), 175 females (winged and therefore virgin) and 7,166 workers characterized by being wingless and without ocelli in distinction to the sexual forms. The normal workers are grouped as 56.2 per cent minors, 30.2 per cent mediae, and 13.5 per cent majors. The normal males and females are very uniform in size and general appearance, the males being larger than the major workers and the females larger than the males. Of the intergrading subcastes of workers, the smaller are darker in color and less tuberculated.

Mutants Classified

The 163 anomalies of this colony include 6 mutant females, 101 mutant workers, 46 gynergates, 1 diploergate and 10 gynandromorphs. Let us consider the mutants first.

A *rugose mutation* is represented by a single dealated female, dark in color like normal females but with rougher integument. She is considered to be the mother of 100 major and media workers having much darker and rougher integument than the bulk of the colony. The reviewer believes that these are intercastes as is suggested by the fact that color and texture of integument of the workers approaches that of the normal female. It is noteworthy also that they are of a large size, majors and mediae, unlike the majority (minors) and that they thus approach the female.

A *pale, spotted mutation* is represented by one dealated and two winged females and a single large worker. Except for the black dots, the color of these females is pale like that of workers. The single large worker suggests an approach to the female in its large size and black dots.

The *scrobiculate mutation* is represented by one dealated "mother" and her winged "daughter," both of small size. They are normal in thorax, abdomen and legs, but their heads are remarkable in showing twelve peculiarities not observable in any of the normal, the two most conspicuous being the cordate shape and the presence of arcuate ridges (carinae) which close the antennal pits (scrobes) posteriorly. Workers and normal females have open scrobes whereas they are closed in the male. However, the author does not regard this as a male character transferred to the female because "the female is decidedly the more variable and genetically the more dominant and progressive sex among the ants as among the other social Aculeates." "The combination in the same individuals of all these (12) deviations from the normal structure and coloration of the *octospinosus* female shows that we are dealing with a complex or cumulative mutation not strictly comparable with the simple mutations described by the geneticists." The reviewer suggests that these may be fe-

male intersexes in the sense defined by Goldschmidt in which the embryological turning-point from female to male has been late enough to involve only superficial head structures. If their small size is significant in this connection, it may be that they started as major workers shifting early to females and later toward the male.

The dealated scrobiculate mutant is regarded as the mother of the ten "gynandromorphs" (male-female mosaics), the 46 "gynergates" (female-worker mosaics) and the single "diploergate" (mosaic of major and media worker).

In the ten "gynandromorphs" the female component is confined to the head (the posterior part in fact) except that in one there is feminization of the genitalia. The heads form a series ranging from very broad as in the female to narrow approaching the male. The antennae are of the thirteen-jointed male type and "the wings are perfectly developed in all the specimens, except *A*, which has been dealated. Since this happens to be the most feminized specimen in the series, the workers may have mistaken it for a female and clipped off its wings, or the individual may have had impulses sufficiently feminine to dealate itself." The reviewer suggests that these "gynandromorphs" are male intersexes of differing grades, showing feminization in more or less superficial traits. Thus they are the reverse of the female intersexes, "gynandromorphs," of the *Cephalotes* colony.

Asymmetry, especially in the more highly intersexual, is to be expected for it is characteristic of many aberrant types. In some cases, as in triploid intersexes, it involves genetic mosaicism brought about by chromosome elimination. More frequently, however, it is due merely to a delicately shifting physiological balance, as in the diploid intersexes of *Lymantria*, the so-called gynandromorphs of birds and many simple mutant types as spotting in mammals, eyelessness, etc., in *Drosophila* and *Habrobracon*.

All the 46 "gynergates" (worker-female mosaics) have bodies indistinguishable from those of major or more rarely of media workers, but the head is in every case dark brown or blackish (a female trait) so that it is easy to recognize them and separate them from the normal workers. The antennae are of the usual eleven-jointed worker or female type. The whole series is roughly divided into three groups which show transitions from more or less symmetrical anteroposterior to very asymmetrical right-and-left segregation of the worker and female characters. None of these shows any trace of ocelli (which are lacking in workers, small in females and large in males) although they are present in the two "scrobiculate mutant females." The author attributes this lack to histological disturbances or "to a strong ocellus-inhibiting factor (perhaps hormonal?) in the worker component of the mosaic." The alternative intercaste interpretation would place them as worker intercastes which began development as workers with a turning-point too late to involve production of ocelli. The closure of the scrobal arches, which occurs in the great majority of these anomalies, is a trait of relatively late developmental determination. The fact that these arches are closed in the male indicates that these intercastes are also intersexes, transgressing the sex boundary in this superficial trait. It is noteworthy that they are of large size, (majors or large mediae) although the majority of the normal workers in the colony are minors. The five "gynergates" having open scrobes may represent regressive fluctuation toward the normal major worker.

The single "diploergate" has the body of a large media worker, but the left side of the head is enlarged, resembling that of a major. This is then a media worker intercaste with a late turning-point toward the major. Thus the intercaste-intersex series may range in order, —minors, mediae, majors, females, males.

Whether the soldier of species with so-called tetramorphic workers may be placed in this series may perhaps be decided by reconsideration of specimens

described under such names as "dinergatandromorph" (soldier-male mosaic), "dinergatogynomorph" (soldier-female mosiac), etc. A "dinergatandromorph" of *Pheidole pallidula* Nyl. described by Vandel* and cited by Professor Wheeler differs from the typical soldier only in its greater size (approach toward female) and its abnormal head which presents on the left side male characters mingled with soldier traits. The left antenna and left eye are intermediate, the two ocelli (median and left lateral) smaller than in the normal male. It seems to the reviewer that some of these traits (reduction in size of ocelli and eyes) are an approach toward the sexual female although others (as in the antenane) are clearly male. It is suggested that this "dinergatandromorph" is a soldier intersex with superficial traits of the female and still more superficial traits of the male. The intercaste-intersex series may then be arranged in order beginning with the female castes,—minor, media and major workers, soldier, sexual female, and finally the male.

The reason for such a great abundance of aberrant types in the *Acromyrmex* colony, as also in that of *Cephalotes*, is undoubtedly genetic. It may be supposed that race mixture is here involved (strong with weak as in Goldschmidt's *Lymantria*) and that different combinations of sex genes within the colony have resulted in intermediate types. The male intersexes, "gynandromorphs," of the *Acromyrmex* colony are presumably haploid, the others diploid, while the female intersexes, "gynandromorphs," of the *Cephalotes* colony and the soldier intersex, "dinergatandromorph," of Pheidole are diploid. It appears that a diploid intercaste may begin development toward the worker end of the series (minor, media, major, soldier, female, male) and later deviate toward the female and even across the sex boundary toward the male, while the haploid intercaste starting as a male deviates toward or beyond the female. Thus the diploid intercaste may or may not be an intersex, while the haploid intercaste is necessarily so. Whether a diploid intercaste starting as a female or a soldier, for example, may deviate in the opposite direction (toward the minor worker) will have to be decided by study of specimens with due regard to embryonic order. This is suggested by the dilute coloring of the females of the *pale, spotted* mutation.

Finally, the moot question of caste-determination seems not vet to have been solved. In the normal ant nest we are concerned not with differences between different species or different races or with genes segregating in hybrid colonies, but with the differences among the diploid castes in a single colony of pure race. The single haploid male caste is without question differentiated genetically. As for the various female castes, the reviewer inclines toward the trophogenic theory. Any blastogenic scheme involving hereditary differences would necessitate some system for maintaining in the reproductive members of the pure race genic differences which might segregate to form the sterile castes. Such is conceivable but doubtful. Differences of size and correlated characters between minors, mediae and majors is readily explained by nutrition. The basis for the wide differences between workers, soldiers and sexual females may not be altogether incomprehensible to the developmental geneticist aware of the far-reaching influence of slight stimuli if applied at critical temperature-effective or nutritive-effective periods. Thus the distended abdomen of the sexual female or the enormous head and jaws of the soldier may be but trophogenically different from the modest proportions of the worker. This trophogenic influence may have taken place before the hatching of the egg.

*VANDEL, A. Etude d'un Gynandromorphe (Dinergatandromorphe) de *Pheidole pallidula* Nyl. (Hyménoptères-Formicidés). Bulletin Biologique de la France et de la Belgique. 65: (1) :114-129.

MONKEY-BUSINESS AMONG THE MORONS

A Review

WHILE reading this book* the reviewer felt a good deal like the farmer whom chance led to investigate an edition of Plato he had fallen heir to. After some immersion in the subject matter, the rustic exclaimed, "Say, this man Plato has a lot of my ideas." Dr. Hooten has in addition lots of ideas that are strictly *sui generis* and a generous supply of trenchant comment upon many subjects. At intervals throughout the text Dr. Hooten may make a sudden sally which scatters sacred cows and he may pursue the bubble reputation even to the canon's mouth, and there prick it.

The order in which the organisms appear in the title illustrates the author's conviction that human evolution may very well be parabolic in nature and already past its apogee. "His (man's) acquisition of high civilization is very recent and perhaps only temporary."

The book is a compilation of nineteen lectures and addresses upon different phases of anthropology which go together rather well in spite of the fact that they were presumably designed as self sufficient units rather than as chapters in a book. Indeed there is perhaps no more convincing evidence of the attractiveness of Dr. Hooten's style than his ability to sustain great interest in Part I, which is made up of nine addresses upon human prehistory. There is only so much human prehistory to begin with, and the subject matter has lost much of its bloom through handling (and manhandling) by prior authors, but Hooten's rendition makes this old time religion the sweetest story ever told.

Part II on the biology of human races, a more esoteric subject under any circumstances, contains in addition results from the author's (and his colleague's) measurements of large numbers of past and present Americans. Part III, dedicated particularly to a general sociological summing up, contains some of the most effective writing upon eugenics that has been done. Eugenics also gets some efficient attention in a number of other places in the text.

"Psyching" the Anthropologist

During the discussion of human prehistory the author digs out for the reader's fascinated gaze the deep-seated nationalistic and psychological attitudes which, in anthropologists, color and shape anthropological conclusions. The German believes that human separation from anthropoid stock is relatively recent and looks with "morbid simian suspicion" upon all fossil men without supraorbitel tori and "bath-tub shaped" jaws. The English tend to separate man from the ape stock in the Oligocene and would like to believe that *Homo sapiens* was at least a Neanderthal contemporary. They go balmy on Lamarckism. The French attitude upon these two important issues is a frank admission that the late Pleistocene Frenchman, like the modern type, is superior to other contemporary Europeans. The author is most sympathetic with the English attitude, divested of Lamarckian excresences, and if he is as English as his given names suggest this may be just a further interesting example of his general thesis that "there are bodily correlates of mental sets."

Basing his opinion upon the premise that physical resemblance is the best indication of kinship, the author is of the opinion that the ancestors of man and the African anthropoids diverged from the fore-brachiators of the Asiatic apes in the Miocene, and that the ancestors of man shifted their interminable search for the more abundant life from the treetops to the ground in the latter part of that same period. They were prompted in this decision he thinks by a voluntary selection of environment rather

*HOOTEN, E. A. *Apes, Men, and Morons.* G. Putnam's Sons, N. Y., 1937.

than because of a dearth of trees to climb. Man's persistent tendency to remain "up a tree" as far as social and economic adjustment is concerned and the rate at which this problem is getting more complex perhaps represents an atavistic spiritual return to his ancestral home.

The author thinks that undiscovered ancestors of man were using eoliths in the Pliocene and that in the early Pleistocene a number of varieties of archaic man were extant, the ancestors of *Homo sapiens* diverging at this time from taurodont stocks that produced Sinanthropus and the Neanderthals. Dr. Hooten was thus greatly interested in Leakey's report of the Kanam mandible and disappointed when an investigation of the paleontological evidence showed it to be leaky. The reviewer is inclined to believe that Dr. Hooten's failure to use this pun indicates his loyalty to the preneanderthal sapiens theory, more than his forebearance. Dr. Hooten does not share Hrdlicka's opinion that we are merely streamlined descendants of Neanderthalers, although he admits that the recent Palestine discoveries of individuals with both Neanderthal and modern characters strengthen that theory.

Homo's Taxonomy

Upon racial matters, Dr. Hooten makes no attempt to mince or weasle words. There are, he admits, no "pure" races but since intraracial mating has been so much commoner than interracial crosses, there are "divisions of mankind, the members of which are distinguished by the possession of similar combinations of anatomical features due to their common heredity." People within even subraces recognize each other as kindred folk even without the blessing of anthropological training. He thinks that the three main racial groups, negroid, mongoloid and white exhibit sufficient average physical differences for subspecific or possibly specific separation, and that average differences in taste, temperament and intellectual abilities might very well be demonstrated if we had techniques for their accurate measurement and used them. He takes issue with those anthropologists and sociologists who make the quaint inference that because we are yet unable to determine the relative sociological or economic worth of racial or national groups that there are no important differences between them. There are, he believes not only important physical differences between even subracial groups of people but probably also, some physical basis for what are supposed to be purely psychological or cultural differences. It is the business of the anthropologist to investigate just such matters with the idea of critical appraisal. "The breakdown of the principal agencies of human improvement . . . is due to the fact that the responsible elements of society are ignorant of the biological basis of human activity as the fundamental element in the social situation."

The author adds example to precept in his material upon aboriginal and modern Americans. His premises, that "race is a matter of physical features" and "involves considerable fixity of physical type," allow the conclusion that careful measurement of numbers of individuals will give the analytical data needed. This seems to demonstrate that the American Indians form a comparatively homogeneous group with predominantly mongoloid characters. There are, however, a number of features like an aquiline nose, fine or wavy hair and certain skull characters which are non-mongoloid in type and presumably pre-mongoloid in origin. Such characters tend to be found either in the eastern part of Canada or the United States or in central or South America, that is to say, removed from the point of immigrant entrance via Behring Sea. The author inclines to the opinion that there was more than one type of immigrant who antedated the all-pervading mongol.

Human Ornithology — Telling the Yale-birds from the Jailbirds

The data upon modern American whites was obtained by measurements of a large number of criminals from

Big Houses in nine representative states, a number of workaday citizens from Boston and Tennessee and a considerable number of trippers to the Century of Progress Exposition who were sufficiently intellectual to visit the anthropometric laboratory and to arrange to undergo measurement there. The author points out that the criminals were particularly entitled to investigation since we have so many of them and since they are even more expensive than war veterans. The less costly and somewhat more inhibited law abiders were used as controls for comparisons and as representatives of samples of the population of our great country.

Nine arbitrary racial categories were made, based on the cephalic and nasal indices, stature, hair and eye color supposed to be characteristic of the several races of Europe and their hybrids. The data were sorted and individuals assigned to these predetermined groups which proved upon statistical test to be valid ones. In order of their occurrence in the combined sample populations the groups were: Nordic-Mediterranean, Nordic-Alpine, predominantly Nordic, mixed Dinaric, Keltic, Mediterranean, East Baltic, Alpine, Nordic. Thus, although the "pure" Nordic is the rarest type in the American population, the statement that physically we are more Nordic than anything else is no myth. The rank order tended to be similar but not identical in the three separate groups (criminal, Century of Progress and East Boston). Where differences occurred they were most obviously attributable to the inclusion of a chunk of foreign material, that hadn't melted yet, in one of the populations: mixed Dinaric in the Boston workaday for example. An "Old American" at outs with society, nabbed, and so in stir, proved to be physically about the same as an "Old American" in the money and out on a holiday trip to the Century of Progress Exposition when caught and measured.

Some great differences were found in similar categories of criminal and noncriminal American in education and type of requited toil. For example, twenty-five per cent of Nordic-Mediterranean criminals had been farmers, miners and so forth and less than four per cent of them had attended any institution of higher learning: Yale to them meant just another challenge to their ability to pick a lock. Less than two and three per cent, respectively, of the Nordic-Mediterranean, Boston and Century of Progress taxpayers were engaged in merely extracting wealth from the ground. The Bostonians were somewhat informed and the Century of Progress group was very well educated.

Different racial categories, whether criminal or not, tended to have different occupational peculiarities and if criminal to commit different sorts of crime. Pure Nordics are forgers and confidence men, Mediterraneans commit crimes of violence against persons, while East Baltic criminals are more liable to be thieves.

The data showed, as would be expected, a tendency for racial synthesis in groups from necks-of-the-woods where long settlement and some isolation had brought about inbreeding and even showed some indication of state types. In time such terms as Hoosier, Hawkeye, or Webfoot may have considerable anthropological significance.

Time to Quit Monkeying

The general thesis of Part III is that, true to his simian character, man has been monkeying with human evolution and must now change his tune, and *manage* if there is to be a continued age of man. Everybody seems to realize this but the public is ignorant of the technicalities and tries to handle the situation by prodigeous efforts all directed to mere improvement of the environment. Technicians, Dr. Hooten opines, like general biologists, anthropologists, geneticists and physicians, either moan like Hamlet about their responsibility and procrastinate or just ignore the whole problem. Dr. Hooten obviously believes that these brave fellows need a good verbal shellacking and lays some of it on with a

gifted brush. He also makes a number of suggestions.

Concerning the biologists he says, "This detachment of knowledge from application . . . is at a maximum in biology which tends to divorce itself wholly from the human animal." Dr. Hooten feels that the proper study of mankind is man. He doesn't believe that eugenists will accomplish much by a frigidly scientific presentation of facts and a Judas-like denial of relationship with enthusiasts who would like to promulgate eugenics with considerable emotional fervor. It is better, he suggests, to make some errors in achieving progress than to achieve nothing, and he considers that critics of eugenics often have ulterior motives and make a good deal out of relatively trivial dangers.

Teaching Old Docs New Pediatrics

The physician gets a whole chapter of consideration and some attention in other chapters. This biological specialist not only knows more about man than any other student of the species but has the special advantages of traditional sanction and of dealing with people when their need of him is paramount. As scientific material has accumulated his opportunities of doing individual good have greatly expanded, but not without a correlative increase in a capacity to do specific harm in nullifying the operation of natural selection. The doctor judges the sick and the dead and sadly lacks a really adequate knowledge of the well and the living. The writer feels that anthropology would leaven medical knowledge if it could supply the latter with an adequate notion of "normal" human variation and other statistical rather than individual methods of appraisal.

Diagnosis would be greatly facilitated by statistical studies of constitution which the skilled diagnostician picks up with experience; a by guess and by gosh! method. Orthopedics should be built upon an adequate knowledge of human phylogeny. The physician has usually been carefully trained in human embryology. Specialists in pediatrics know something about development in infancy and childhood although they have engulfed undigested masses of figures supplied by ambitious amateurs who get growth curves by lining 'em up and measuring them without regard to race, creed, or previous condition of servitude. Neither amateurs nor physicians, says Hooten, have at their disposal an accurate statistical picture of the developmental changes which take place in the post-adolescent stage and during maturity, that is to say, no accurate picture of the age groups in whose hands the destiny of the world is placed. Dr. Hooten suggests that the creation of the medical specialty of geratology for this. He believes that physical anthropology and medicine could produce the discipline of clinical anthropology dedicated to the study of *well* human beings. The anthropologists would get the satisfaction of statistically investigaitng something worth while and the physicians would get a morphology based on the flow of developmental tendencies through bodies rather than on the anatomical atlas.

Cassandra *vs* Pollyanna

Although Professor Hooten is quick to notice the ways in which our time is out of joint there are lots of things he approves of. He likes intelligent students, accurate comparisons, debunkers, alliteration, biblical illustrations and bon mots. He seems to think a lot of dentists, W. K. Gregory and Sir Arthur Kieth. He is especially critical of bawling demagogues, snuffling sentimentalists, intellectual Pharasees, politicians and veterans who bleed the fatherland. He appears to be rather pessimistic about a world that lets all these latter types get along so superlatively well. He admis having been called a Cassandra and remarks:

"If I have to be identified with female literary characters, I prefer the evil-foreboding role of the Greek prophetess to that of a fatuous Pollyanna, dispensing shallow cheer." There is a fine, prophetic, *prepare ye the way of the*

Lord flavor about statements like: "There can be no miracle whereby the group intelligence transcends the possibly moronic mean of its constituent members."

But perhaps Professor Hooten is most in character as a sagacious and exacting mentor who realizes the need of thinking things through to their ultimate conclusion and believes in trying to make others do the same. The reviewer is here reminded of an early episode in the life of Mr. Midshipman Easy (a character used as an example by Dr. Hooten himself). Young Master Easy, who would learn nothing at home, was sent to school where he was sufficiently daunted by strange surroundings and the hard eye of the schoolmaster to learn *A* but he wouldn't budge as far as *B*. There followed a rather painful scene at the termination of which little Jack proved an apt and willing student. The biologist who spends adolescent primates' time in preparatory preludes to human biology and teaches none of the latter; the educator who puts new wrinkles in his methodology and none in the brows of the pupils; the physician who gives entire loyalty to his patients but feels he owes none to the patients' species, and the geneticist who won't commit himself on the sociological implications of hereditary laws; all these are the intellectual brothers of little Jack Easy. Most readers of *Apes, Men and Morons* will want Dr. Hooten to continue his spirited comments on such individuals until a lot of them say "B." The reviewer hopes he lays it on until the lot of them give loud vent to that good old primate half-grunt of submission which in our tongue sounds like one's father's brother.

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Bud Mutation Bibliography a "Supplementary Document"

THE supplementary bibliography of the article "Bud Mutations and Bud Selection," by A. D. Shamel and G. S. Pomeroy which appeared in the Journal of Heredity, Vol. 27, 1936, pp. 486-494, has been deposited with the American Documentation Institute. This bibliography of 185 titles was issued as a mimeographed supplement. It is now made permanently available, and readily cited as Document 1087 of the American Documentation Institute, 2101 Constitution Avenue, Washington, D. C. Copies can be obtained from the Institute by giving the order number (1087) and remitting 33c for microfilm, or $1.50 for photoprints readable without optical aid. For detailed information regarding the microfilm service, and the auxiliary publication service recently inaugurated, write the American Documentation Institute.

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Civil Service Announces Geneticist Examinations

THE United States Civil Service announces unassembled examinations of interest to Poultry Geneticists as follows:

(1) *Senior Geneticist (Poultry)*, $4,600 a year; (2) *Geneticist (Poultry)*, $3,800 a year; (3) *Associate Geneticist (Poultry)*, $3,200 a year; (4) *Assistant Geneticist (Poultry)*, $2,600 a year. The date of all these examinations is June 20. A College Degree and considerable practical experience is necessary. Application forms and literature setting forth the requirements may be obtained from the Civil Service Commission, Washington, D. C. Ask for examination of above title, No. 55. Similar examinations (Nos. 53 and 54) are being given for Veterinarian and Poultry Husbandmen on the same date.

A PEDIGREE OF SYMPHALANGISM

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SYMPHALANGISM is a term used by Cushing[1] to designate the fusion of the proximal interphalangeal joints. That ankylosis of the joints in this hereditary defect may not be confined to the first and second phalanges of the hands has been demonstrated by Hefner[4]. He reports a study in which the second and third phalanges of the fourth finger of the right hand in one individual were fused in addition to the union of the first and second phalanges of all fingers. Flat feet seem to have been generally associated with symphalangism, as it has been mentioned in papers by Walker[6], Cushing[1] and Hefner[4]. A shortened hand, described as squatness by Hann[3] has been considered by some as associated with symphalangism. However, Inman[5] specifically points out that in the case investigated by him there was very little, if any, shortening of the digits. Furthermore, Inman, describes a boy in which but two fingers, the second and fifth, on each hand are affected while on each foot four toes show fusion of the joints. The work of Duncan[2] also records the presence of the deformity of the feet in which the second joints were stiff.

As will be observed from the above reports, symphalangism is variable in its physical expression; but as to its inheritance, there seems a general agreement that it is a simple Mendelian dominant. Several other skeletal anomolies such as brachydactylism and syndactylism are considered to be dominant characters. Not enough investigations on symphalangism have been completed to make possible the publication of a monograph as has been done in the case of syndactylism. In fact, hereditary ankylosis of the joints seems to be rather rare; and inasmuch as its physical expression is variable, it was thought worthwhile to report another pedigree of this defect which exhibits some physical differences from those previously reported.

This case of symphalangism has been traced through six generations (Figure 17.) In the course of six generations there are seventeen out of nineteen individuals affected with the trait. It was impossible to obtain x-ray photographs of the informant (V-1) of this study, but the photographs (Figure 16) show very well the characterisic condition of the defective hands in this family. At the point between the first and second phalanges, where the joint should appear, it will be observed that the skin is perfectly smooth, giving no indication of a joint, and that the bone is smooth to the touch. However, because the fourth finger of the left hand has been broken, a slight prominence on it appears in the photographs. On both hands the index finger gives some indication of a joint being present as there is a hint of transverse cutaneous wrinkles of the proximal interphalangeal joints. There might be a vestigial joint present, but this cannot be positively determined without an x-ray photograph. The little finger articulates only with the metacarpel, the interphalangeal joints all being absent. At the junction of the middle and distal phalanges, the fifth finger is bent mesially to a very marked degree. This curvature of the little finger is present in all individuals of this investigation except V-3 and VI-1. Not all members of the family in which the fifth digit is crooked show this condition in such a striking form as V-1 of Figure 16. The deformity is symmetrical with the exception of case V-3; this girl does not suffer ankylosis in any of the joints of the index finger of the right hand. The only individual

SYMPHALANGISM OF THE HANDS

Figure 16

The upper picture shows that the middle joints of the second, third and fourth digits cannot be flexed. The little finger shows "double symphalangism" as both interphalangeal joints are fused. Note the mesial bending of the fifth finger in both hands. The lower photograph is of a side view which shows clearly the cutaneous wrinkles of the thumb, indicating that it is normal. A slight prominence appears at the proximal interphalangeal joint of the fourth finger of the left hand, due to a fracture. The fingers of the right hand illustrate the peculiar bending of the fingers of a symphalangous hand. Rarely can one with normal hands bend the distal interphalangeal joints without some flexion of the proximal joints. Note, with the exception of the fifth digit, the characteristic column-like appearance of the affected fingers.

SIX GENERATIONS OF SYMPHALANGISM

Figure 17

A pedigree-chart showing the inheritance of symphalangism in a family of which seventeen out of nineteen related individuals were affected. The pedigree suggests dominance of the defect, and it could be simple Mendelian in its inheritance.

(VI-1) in the last generation is a baby girl about 3 months old and it cannot be clearly determined what the condition of her hands is. However, it can be seen that some anomolous condition exists but whether it is typical symphalangism cannot be determined. This girl (VI-1) has been designated in the chart as symphalangous; for with the family history which she has, it seems highly probable that she will prove to have this character.

Discussion

As discussed above, in some symphalangous families the shortened hand seems characteristic. That is not true of V-1 of this study; in fact, one might judge from Figure 16 that the digits were longer than usual. But when it is known, however, that this young man is of large stature, being over six feet in height, it will not be difficult to believe that the hands are in proportion to the rest of the body. There was no observed tendency anywhere in the defective members of this family to possess shortened hands. Neither were flattened feet associated with those of this family who had stiff fingers; nor were any found to suffer from fused digits of the feet. On the other hand, this family is characterized by an ankylosis of the third and second, as well as the first and second phalanges, of the fifth digit, a condition which has not been generally found to exist in previous studies of this trait. It is evident that symphalangism varies in its expression not only within a given family, but that there are also modifications of the trait found peculiar to different families.

In view of the variability of the trait, it seems desirable to broaden the definition of symphalangism to mean a fusion of any of the joints of fingers or toes.

It is interesting to note that the third, fourth, and fifth fingers are affected in the only individual who has less than four involved. Thus, when three fingers are malformed, the index alone is capable of normal flexure. Further, the only finger in which two joints are fused is the fifth. Hefner suggests that since the mesial phalanges are the last to ossify in development, a lack of the usual inhibiting influence might be conceived to be the cause of the extreme ossification here, resulting in the ankylosis of the proximal joints. He also adds that the greater frequency of fusion in the fifth digit of the hand may be correlated with the late time of ossification in the first and second phalanges of this digit. In all probability, variations in the expression of this abnormality are due to some modification of the embryological process. Certainly there is no necessity for assuming a modification of the gene to produce the differences in the manifestation of this trait as has been postulated. Hefner's developmental hypothesis would not seem to be applicable in a case where the second finger is affected but not the third and fourth. However, it is known that in the embryogeny of an animal the time at which a process may occur is frequently disturbed by irregularities. From Stiles' (in press) work on intermediate aphids he has found that the usual time at which an organ is determined may be so variable that in certain instances there will be a reversal of the times at which two differ-

ent organs are established. This occurs under conditions which would make any modification of the gene an extremely unlikely cause.

Of the individuals studied, most were accustomed to manual labor, and they did not seem to experience any great inconvenience because of their peculiar inheritance. The young man, V-1, whose hands are illustrated, is active in athletics, playing baseball, basketball and football. Of course there are special kinds of work for which this family would not be qualified, but the fact that the thumb functions normally is of great assistance to them. The mental condition of the family seems to be about what might be expected from a middle-class group; certainly, there is no evidence of any mental defectiveness correlated with the peculiar skeletal structure.

If the assumption is made that symphalangism is due to a dominant autosomal factor, an inspection of the pedigree chart shows the following Mendelian facts. In the first generation the affected woman (I-1) could have been either heterozygous or homozygous for the defective gene as she has only one child (II-1) which is symphalangous. The girl (II-1) of the second generation must be heterozygous for the trait as she had a normal father. Likewise the individuals III-2, IV-1, IV-4, IV-9, and V-5 must also have been heterozygous for fused fingers. From the known heterozygous matings for the defect with what are assumed to be homozygous recessives for normal digits, there are fifteen affected offspring and two normal. This is in very poor agreement with the expected ratio of 1:1, if the trait is a simple Mendelian dominant as Cushing's charts indicate. Certainly this pedigree suggests dominance for the trait in question; and the number of individuals involved is so small, that its mode of inheritance could still be simple Mendelian. There appears to be no evidence that a sex-linked, sex-influenced, or sex-limited factor is responsible for this character.

Summary

1. Symphalangism is defined as a hereditary fusion of the phalangeal joints of the digits.
2. Symphalangism is variable in its physical expression between different families and also between individuals of one particular family.
3. There was no evidence of any relation between either brachydactyly or flat feet and ankylosis of the phalangeal joints in this study.
4. The trait has been studied from parent to child through six generations.
5. An inspection of the pedigree makes it appear possible that the trait is a simple Mendelian dominant although the ratio of symphalangous to normal individuals is far from meeting the expected ratio in this family.

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HYDROCEPHALUS IN SWINE

A New Lethal Defect

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TWO types of hydrocephalus have been recognized by MacCallum.[4] The first is due to an occlusion of one of the interventricular canals, usually the acqueduct of Sylvius, and as a result fluid accumulates in the ventricles anterior to the occlusion. This causes a distension of the cerebral hemispheres, due to the internal pressure, with a corresponding increase in the size of the head. The second type is external, or communicating, in nature. The fluid accumulates outside the brain in the subarachnoid spaces. The pressure, due to the accumulated serum, in this type causes a partial collapse of the brain so that it occupies the anterior and ventral portion of the cranium. The condition reported herein is of this latter type.

Most cases of hydrocephalus that have been reported are sporadic in nature. It has been described as such in cattle, man, chickens, dogs, and rats (cited by Clark[2]). These sporadic teratologies are of interest for they show many modifications of the two basic types of the hydrocephalic condition. Associated with the hydrocephalus condition may be other anomalies, such as ectopic organs, micro- and anencephaly.

Clark[1] and Zimmerman[6] have reported an inherited hydrocephalus condition in mice. Both workers found the condition was caused by a single recessive gene. Clark[3] showed, furthermore, that different genes were responsible for the two strains which had been studied. In an anatomical study of the defect in his strain of mice Clark[2] found it was of the occlusion type; the acqueduct of Sylvius being the site of the occlusion. In this paper he summarizes the literature dealing with the anatomical nature of the defect and discusses the relationships of the findings that have been reported.

Description of the Defect in Swine

The type of hydrocephalus herein reported is found in Duroc Jersey hogs and is of the external type. The fluid is found outside of the brain in the subarachnoid spaces. The condition is lethal in swine. The young pigs are either born dead or die within two days after birth. If the pig has an excessively large head the sow almost invariably has to be assisted during parturition.

As pointed out by Clark[2,3] for mice, not all the animals are affected to the same degree. Wright[5] also finds a graded series in his guinea pig monsters. He explains the graded state as being conditioned in part by the time of action of the genes involved. The earlier the genes manifest themselves the more pronouncd is the abnormality. Whether the variation in the degree of hydrocephaly in swine is due to the time action of the genes is not known. A graded series was found varying from animals possessing an almost normal appearing head to animals whose head is most abnormal in appearance. In swine, however, two other characteristics made it easy to detect the hydrocephalus individuals. The affected animals were characterized not only by their enlarged heads, but also by their extremely light coat color and their short tails. The coat color of the hydrocephalus individuals was, in all but three instances, a very dilute red with a silvery sheen to it. The tail varied from no tail at all, 0.0 cm, to 1.8 cm with a mean of $0.97 \pm .06$ cm, while the tail of the normal animals ranged 5.5 cm to 9.4 cm with a mean of $7.2 \pm .03$ cm. Even in animals whose head shape appeared normal, if they had a short tail and a light coat color, fluid was found in the cranium upon necropsy.

In some cases the ears of the hydro-

cephalus animals were somewhat reduced in size. In certain animals one ear was much smaller than the other. Whether this is a part of the same complex of the expression of the hydrocephalus gene has not been determined.

Immediately after death the hydrocephalus animals were placed in the freezing room of the refrigerator at a temperature of about 15 degrees F. where they were frozen. They were held in this state until it was convenient to examine them. They were removed from the refrigerator to the laboratory a short time before the measurements and examination were made. This allowed the outside to thaw, but did not melt the frozen serum. The frozen fluid could be lifted out and weighed without difficulty. If any of the serum had melted it was poured from the cranium and weighed with the frozen part.

In the most markedly affected animals the skull was dome shaped. It was wider, longer and slightly higher in the crown than the normal skull. In profile view it resembled a bulldog head (see Figure 18). The eye sockets were flattened laterally by pressure from within the cranium. The length from front to rear (the long axis of the eye socket) varied from 1.2 to 2.5 cm with a mean of 1.7 $\pm$ .04 cm, while the normal orbit ranged from 1.8 to 2.3 cm with a mean of 2.0 $\pm$ .04 cm. The difference between the means is 0.3 $\pm$ .06 cm, which is statistically significant. The height of the orbit (the short axis), from the zygomatic arch to top of the socket was also reduced below normal in size. The height for the defective pigs ranged from 1.0 to 2.0 cm with a mean of 1.3 $\pm$ .03 while the normal animals varied from 1.6 to 2.0 with a mean of 1.8 $\pm$ .04 cm. The difference between the means is significant being 0.5 $\pm$ .05 cm. The eyes of most of the hydrocephalus individuals were less than normal in size. In most cases they were no larger than an average size garden pea.

When the skin covering the head was removed, changes in the texture of the bones were noted. The parietals were the bones most often affected with the

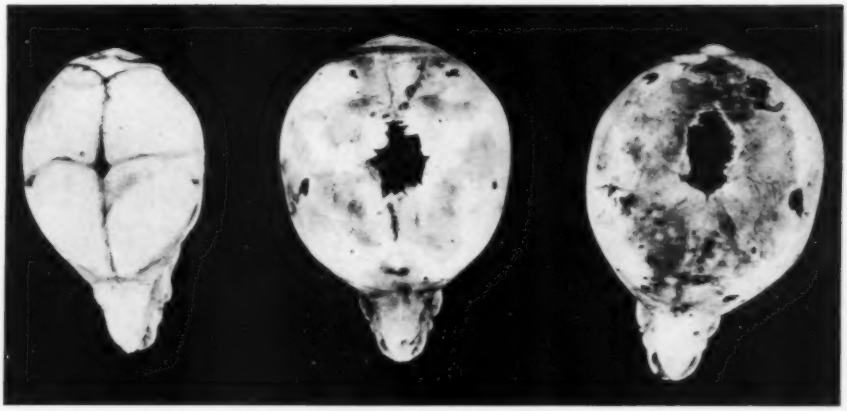
HYDROCEPHALOUS PIGS

Figure 18

These pigs were out of 70 S'33 and were sired by Elmer's Pride. Note the light coat color, lack of tail, and the fullness of the posterior part of the skull, a group of characters displayed by nearly all the affected pigs.

frontals ranking second in degree of change. In the most severe cases the sutures on the top of the head were not fused and an open fontanel was often found between the parientals and frontals. Figure 19 shows one of the skulls thus affected. The parietals and frontals were usually thinner than normal and in many instances they were dotted with holes that appeared to be covered only by a connective tissue membrane. These holes varied in size from pin points up to 5 mm. in diameter.

The difference in the size and shape of the hydrocephalus heads as compared to normal heads is seen in Table I. The



DORSAL VIEW OF HYDROCEPHALOUS SKULLS

Figure 19

The skull on the left represents a medium degree, the other two show a high degree of the defect. Note the paper-like thinness of the bones of the two on the right, and the lack of fusion of the sutures in that at the left.

statistics were calculated from ungrouped data. An examination of the table shows that more variability is present in the hydrocephalus population. There are several causes for this variability: (1) the size of the pig, the body size of the animals varied from very small to exceptionally large; (2) degree of hydrocephalus, some of the animals' skulls looked normal from the outward appearance while others showed a high degree of abnormality. The hydrocephalus animals had heads in which the parietals were longer than normal; also the heads were longer and wider than normal. The height of the cranium as measured from the zygomatic arch to the junction of the parietals and frontals was not significantly different from the height of the heads of normal pigs. The junction of the parietals and frontals was chosen as one point from which to measure because it was definite and could be quickly and easily seen even though the highest point of the hydrocephalus skull was posterior to that point.

From the external side the bones were smooth and normal in texture, although in many animals they were obviously thin as was shown by the presence of holes and by dark appearing areas where the contents of the cranium showed through the bone. The inner surface was often uneven and the bone was found to vary in thickness. Occasionally solid white circular areas were seen on the outer surface of the skulls. When these areas were examined from within they were found to be much thicker than the surrounding bone tissue.

The distension and dome shaped appearance of the skull was caused by an accumulation of fluid within the cranium. The fluid was outside the brain, underneath the dura mater. The pressure of the fluid on the brain had caused the partial collapse of the hemispheres. Instead of being large and rounding over the cerebellum as they normally do, they were lying in the antero-ventral portion of the brain box. In the cases diagnosed as of medium and high degree, the hemispheres did not extend back of the parietal-frontal suture, as was observed in the lower grades. In the higher degrees the brain was pushed both anteriorly and posteriorly, leaving very little brain tissue lying in the center of the cranium.

A number of those animals which

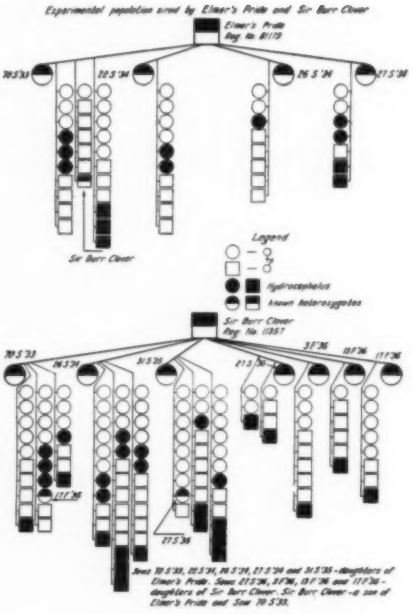
were born alive stood with difficulty. Their joints were stiff and they quivered all over. When placed on their feet they squealed as though in pain and were unable to coordinate their movements. They kept their jaws tightly closed and it was impossible to get them to suckle the sow. Invariably they died within the first two days after birth.

Types of Matings

The hydrocephalous condition was found in the Duroc Jersey breed of swine. All matings were between purebred animals. The hydrocephalous pigs all trace to one boar, Elmer's Pride N-81179. He was used as the herd boar for several years and the defect first appeared when he was mated to his own daughters. The first hydrocephalous animals were found in a litter out of sow 70, the litter as well as sow 70 were sired by Elmer's Pride. Subsequent sire × daughter matings also produced hydrocephalous pigs. None of the sows nor Elmer's Pride gave any outward indication that they carried the hydrocephalous condition.

When the first defective animals were found it was assumed, if the defect proved to be genetic in nature, that the gene causing the hydrocephalous character was a simple recessive. Four daughters of Elmer's Pride were saved and mated back to their sire. These sows Nos. 70, 22, 26, and 27 produced in 6 litters 53 animals of which 13 proved to be hydrocephalous. This is a very close approximation of a three to one ratio which would be expected from this back cross type of mating if the character were caused by a recessive gene. Further evidence of the recessive nature was found in the fact that not all the daughters of Elmer's Pride when back crossed to him produced defective pigs in their litters.

Sir Burr Clover 11357, an inbred son of Elmer's Pride out of a sow 70, was saved to replace the old boar. He, when mated to his dam and to sows related to her through Elmer's Pride, has sired litters in which hydrocephalous pigs



PEDIGREES OF HYDROCEPHALUS
Figure 20

All hydrocephalous pigs were sired by Elmer's Pride, or his inbred son, Sir Burr Clover.

were found. He has also been mated to his daughters and defective pigs were found in these litters.

The accompanying charts (Figure 20) show the relationship which the animals bear to each other. All of the animals trace to Elmer's Pride. Either Elmer's Pride or his inbred son, Sir Burr Clover, is the sire of all the litters in which hydrocephalous animals have been found. For the sake of brevity and clarity only those matings in which hydrocephalous pigs were farrowed are shown in Figure 20.

Discussion

The experimental population consists of 20 litters containing 178 individuals. Six of these litters (53 animals) were sired by Elmer's Pride and 14 litters

(125 individuals) were sired by his son Sir Burr Clover.

During the course of the experiment, two cases of hydrocephalus have been noted, which are not part of this study. One of these was in a Poland China litter, and is evidently one of the sporadic teratologies which are observed from time to time. The other was in a Duroc Jersey litter out of a daughter of Elmer's Pride but sired by an unknown boar (the record of the mating was not recorded) and so has not been included in Table II.

Table II is a summary of the results obtained in this experiment. Eleven of the litters were the result of father-daughter matings; three, sow 70 mated to Sir Burr Clover, were mother-son matings; and the remaining 6 were produced by mating inbred daughters of Elmer's Pride to his inbred son. All of the litters, no matter how they were produced, are the result of mating heterozygous animals together. This type of mating should give a 3:1 ratio if the character in question is caused by a recessive gene. Twenty litters comprising a total of 178 pigs were produced. Of these 42 were hydrocephalous and 136 were normal. This is a deviation of 2.5 from the expected 3:1 ratio. This deviation gives a χ^2 of 0.18727 with a P between .5 and .7.

The distribution of the sexes in the hydrocephalous animals is about equal, —there being 22 males and 20 females. There is, therefore, no indication that the character is sex limited. From the numbers and distribution of the sexes in the litters and from the types of matings made, the gene causing the hydrocephalous character could not be sex linked. If the gene was borne on the sex chromosome the boars should have shown at least one character of the syndrome. None of these were seen in either of the sexes.

That Elmer's Pride is responsible for the hydrocephalous syndrome appearing in the herd is seen from the fact that it did not occur before he was used and until he was mated to his daughters. That he was heterozygous for the condition is seen from the fact that only part of his daughters produced defective pigs when mated to him.

The fact that there are three associated characters, hydrocephalus, light coat color, and short tail forming a syndrome is of interest. The three characters may be explained as being merely the mani-

TABLE I. Frequency Distribution of Measurements Taken on Normal and Hydrocephalous Animals

Part	Length in Centimeters	N.	Mean	S.D.	Differ.
Tail	.5* .6 .7 1.0 1.3 1.6 1.9 2.2 2.5 2.8 3.0				
Hydrocephalus	1 4 9 13 7 3 1	39	1.38 ±.06**	0.36 ±	0.02 .09
Normal	1 2 4 2	18	7.08 .03	1.89	
Orbit Length	1.0 1.4 1.8 2.2 2.6				
Hydrocephalus	2 19 14 2 1	38	1.74 .04	0.24 ±	0.02 .06
Normal	10 8	18	2.06 .06	0.13	
Orbit Height	1.0 1.4 1.8 2.2 2.6				
Hydrocephalus	16 17 4 1	38	1.39 .04	0.24 ±	0.02 .06
Normal	12 2	18	1.69 .03	0.12	
Parietal-Frontal to Parietal Occipital	1.0 1.2 1.4 1.6 1.8 2.0 2.2 2.4 2.6 2.8 3.0 3.2 3.4 3.6				
Hydrocephalus	2 2 3 10 6 7 4 1 4 0 1	35	2.02 .11	0.69 ±	0.05 .13
Normal	10 4 1	18	2.32 .04	0.17	
Cross Sinus-rarum	3.0 4.1 4.4 4.7 5.0 5.3 5.6 5.9 6.2 6.5 6.8 7.1				
Hydrocephalus	4 5 10 4 3 2 2 4 1 1 1	39	4.24 .13	0.79 ±	0.05 .09
Normal	8 6 1	18	4.69 .05	0.20	
Frontal-Nasal to Parietal-Occipital	3.1 3.4 3.7 4.0 4.3 4.6 4.9 5.2				
Hydrocephalus	2 2 11 3 6 7 3 3	39	4.12 .08	0.55 ±	0.03 .10
Normal	6 4 2 2	18	3.92 .05	0.21	
Zygomatic Arch to Parietal-Frontal	5.7 6.0 6.3 6.6 6.9 7.2 7.5 7.8 8.1 8.4 8.7				
Hydrocephalus	2 10 3 5 7 3 1 1 0 0 1	33	6.98 .09	0.54 ±	0.04 .09
Normal	5 8 5	18	6.89 .05	0.19	

| | Weight in Grams | | | |

fold effects of a factor, or they may be assumed to be caused by very closely linked genes. In support of this latter assumption is the fact that three individuals were observed which did not have the light coat color. One of these was a deep cherry red, while the other two were medium reds. These three instances may also be explained as being normal overlaps. The more probable explanation is that the syndrome is the manifold effect of a factor, the three exceptions in coat color being due to normal overlaps or to errors in classification. The possibility, however, of extremely close linkage cannot, with the present data, be entirely ruled out.

The animals produced by mating Sir Burr Clover with his dam, daughters, and half sisters have merely strengthened the proof of the hypothesis formulated previously, namely, that the hydrocephalous syndrome is caused by a single recessive gene. Of the 125 animals sired by Sir Burr Clover, 96 were normal and 29 were hydrocephalous. This is a deviation of 2.25 from the expected 3:1 ratio.

Since Elmer's Pride was purchased when young from a purebred Duroc Jersey breeder there is no way of determining how long ago the original hydrocephalous mutation occurred nor how widespread the defect is in the Duroc Jersey Breed.

The symbol which has been chosen to designate the recessive gene hydrocephalus is *h* with the symbol for the normal condition being *H*.

Summary

This is the first time the lethal hydrocephalus has been reported as an inherited trait in swine. Accompanying the hydrocephalous character is a dilution of the coat color and a marked diminution in the length of the tail.

The hydrocephalus is of the external type, the fluid being found in the subarachnoid spaces. The condition is lethal in swine, the young pigs either being born dead or dying within two days after birth.

The goodness of fit between the observed and expected 3:1 ratio ($\chi^2 = 0.18727$) proves that the hydrocephalus syndrome is caused by a single recessive autosomal gene which is designated by the symbol *h*.

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